DIV. OF HERPETOLOGY

HERPETOLOGICA

Journal of the HERPETOLOGISTS' LEAGUE
Established in 1936 by Chapman Grant

President, Alan E. Leviton. Vice-President, Max M. Hensley.
Secretary-Treasurer, John M. Legler. Editor, Wilmer W. Tanner.

Published Quarterly (Spring, Summer, Autumn, Winter.). Entered as second-class matter at the post office at Provo, Utah.

Published at Brigham Young University; Provo, Utah.

Vol. 16 Dec. 30, 1960 No. 4

UNIVERSITY OF MICHIGAN
JAN 17 1961
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Eggs and Larval Development of the Treefrogs *Hyla crucifer* and *Hyla ocularis*

KENNETH L. GOSNER AND DOUGLAS A. ROSSMAN

The present paper describes previously unrecorded life history stages of the southern spring peeper, *Hyla crucifer bartramiana* Harper, and supplements existing accounts of developmental stages of the little grass frog, *Hyla ocularis* Bosc and Daudin. Eggs of both forms were obtained from mated pairs collected by the junior author who reared a considerable part of the *bartramiana* material and the early stages of *ocularis*. Two lots of live eggs, shipped to the Newark Museum, were inadvertently combined on arrival; the tentative re-segregation of this material shortly after hatching as 2 *ocularis* and 55 *bartramiana* was confirmed by subsequent events and testifies to the fact that the larvae are distinguishable at an early stage. Two *ocularis* were reared through transformation as was part of the *bartramiana* series; the remaining peeper larvae were preserved in two lots at different stages. All of the material studied is now in the collection of the Newark Museum.

Hyla crucifer bartramiana Harper

Adults collected January 2 and February 28, 1959, 1.1 mi. SW Gainesville, Alachua County, Florida. Offspring of two matings provide complete laboratory-reared developmental series from eggs through metamorphosis. Minor differences in the eggs and larvae of the northern and southern races of the spring peeper were found.

Eggs: Eggs are laid singly as in *c. crucifer*. The mean diameter of the vitellus in six eggs is 1.13 mm., range 1.09-1.12, (*c. crucifer* 0.90-1.10), and the diameter of the single jelly envelope is 2.56 mm., range 2.45-2.80 (*c. crucifer* 1.40-2.00); data for *c. crucifer* are from Livezey and Wright (1947). Measurements of New Jersey material were found to be within the above ranges with possibly a slightly

greater mean diameter of the jelly envelope. Because of their larger jelly coats, *bartramiana* eggs key out to "*Acris g. gryllus*" in Livzey and Wright's résumé, but the vitellus of *Acris* was given as 1.0 mm. or less. Stages in the embryological development of *bartramiana* are essentially the same as those of *Hyla regilla* as figured by Eakin (1947). The eggs hatched in about 5½ to 6¼ days at room temperature. Dimorphism in egg color was noted; the majority had the animal pole light chocolate brown and the vegetal pole creamy yellow, but one sample was brownish grey and dirty yellowish white. A similar color dimorphism occurs in eggs of New Jersey *crucifer*.

Larvae: Larvae of the southern form average about 8-10 per cent larger than those of New Jersey peepers. The mean length at hatching, about stage 20, was 4.46 mm. in *bartramiana* compared to 4.21 in the nominal race. Harper (1939) reported *bartramiana* larvae which reached 39 mm., while the largest New Jersey *crucifer* tadpole measured by Gosner and Black (1957) was 34 mm. (Wright and Wright, 1949, gave 33 mm. as the maximum for this subspecies.) Relating these data to the size-staging curves given by Gosner and Black (1957), we estimate the curve for *bartramiana* to lie somewhat less than midway between the curve for northern *crucifer* and *Hyla versicolor*. The smallest stage 25 (operculum complete) larva of *bartramiana* was 7.08 mm. in length; and the smallest with detectable limb buds (stage 26) was 11.9 mm. (For a simplified table of anuran larval stages see Gosner (Herpetologica Vol. 16:183-190).

Adhesive organs are bifid at hatching and their scars disappear before larvae reach stage 26. The present sample probably does not show the full development of external gills; one stage 22 larva has the lower gill with two sub-equal branches and the much smaller upper gill unbranched. The gills are short and inconspicuous.

In coloration and pattern *bartramiana* tadpoles are similar to and perhaps indistinguishable from *crucifer*. For identification purposes pigmentation of the lateral surface of the tail musculature appears to be most useful. Hatchlings are light brown and cream without detectable tail pattern. For a period during stages 21-25 most of the tadpoles develop a bicolored tail pattern, the ventral quarter or less of the musculature being unpigmented. Subsequently this light stripe disappears leaving the lateral surface more or less evenly pigmented except on the ventral margin. The dorsal ridge may be irregularly patterned, particularly in young larvae, with light spots, streaks, or even a somewhat conspicuous stripe. These markings usually are not sharply defined and many older tadpoles have the dorsal ridge evenly pigmented. In life a reddish, golden, or yellowish pigment occurs in the latter area, the color being bright in early stages and usually fading thereafter.

Dark flecks appear in the tail fins as early as stage 28. These increase as reticulations or blotches during larval development. Harper (1939) noted the absence of dark tail-fin blotches in field-

collected *bartramiana,* but these markings vary in *crucifer* and may do so in the southern race as well.

Pigmentation of the larval head and body in the northern and southern races is similar. Pattern is initially dependent on pigment in deep tissues. At this time melanophores are evenly distributed over the top and sides of the body without indication of a postocular light stripe. With the development of surface melanophores, lipophores, and iridophores, the tadpoles assume an olivaceous tinge and show an indistinct postocular light stripe. Rounded dark spots appear between larval stages 29 and 31. The ventral surface is stippled with dark pigment from the earliest larval period. This pigmentation is particularly heavy on the chest and throat and in most larvae it extends well over the abdomen except posteriorly near the midline. Individual stipples are fused into irregular streaks in many mature larvae.

In addition to being larger over-all than *crucifer* larvae, those of *bartramiana* show minor differences in head-body proportions. By use of head-body length as divisor the following ratios are obtained from a series of eleven *bartramiana* tadpoles at stages 30-37. Figures in parentheses are means for New Jersey *crucifer* at equivalent stages: snout-spiracle 0.59-0.78, mean 0.70 (0.77); interocular 0.43-0.49, mean 0.46 (0.49); internasal 0.19-0.23, mean 0.21 (0.21); tail muscle depth 0.20-0.29, mean 0.23 (0.28); eye-snout 0.20-0.27, mean 0.23 (0.25); oral disc 0.19-0.25, mean 0.22 (0.23); total length 2.63-3.16, mean 2.85 (2.78). There is overlap in these ratios between larvae of the two races.

The form of the oral disc in *bartramiana* is similar to that of *crucifer* as figured by Wright (1914). Papillae are single above the sides of the first upper labial tooth row and irregularly doubled laterally and ventrally. When the labial tooth formula is 2/2 the papillary fringe is continuous below, when 2/3 a gap is usually present. At stage 25 the formula is usually 2/2, but some specimens of pre-stage 26, 10.5 mm. long possess 2/3. The present sample is too small to estimate the frequency of 2/2 variants in the southern population; of 48 mature specimens examined 10 have the formula 2/2. Minor differences exist between *bartramiana* and *crucifer* in ratios of oral measurements. By use of the length of the first upper labial tooth row as divisor the following ratios are obtained from 10 larvae at stages 30-37; figures in parentheses are means for New Jersey *crucifer;* papillary free gap on upper labium 0.52-0.71, mean 0.63 (0.71); second upper labial tooth row 0.32-0.52, mean 0.46 (0.44); gap between second upper labial tooth rows 0.09-0.19, mean 0.13 (0.18); horny beak 0.59-0.65, mean 0.60 (0.54); first lower labial tooth row 0.63-0.76, mean 0.70 (0.72); second lower labial tooth row 0.81-0.95, mean 0.87 (0.85); third lower labial tooth row 0.05-0.26, mean 0.10 (0.21).

Metamorphosis: The minimum time required for larval development in laboratory groups was 45 days. Prior to the appearance of front limbs the dorsal body spots become fused and modified to form an adult-type pattern; when the young leave the water they are miniature peepers in appearance. The more massive cruciform markings ascribed to the southern race are apparent in newly transformed *bartramiana*. Sixteen transforming young average 10.3 mm. in snout-vent length, range 9.4-11.0. These are slightly smaller at an equivalent stage than New Jersey *crucifer* which average 10.9 mm.; the difference is not considered significant since both smaller size and longer larval period in the laboratory material may have been due to environmental conditions.

Hyla ocularis Bosc and Daudin

Adults collected February 8 and 28, 1959, 1.1 mi. SW Gainesville, Alachua County, Florida. Offspring of these matings provided a preserved series of early developmental stages, and notes were made on two individuals reared through metamorphosis. In addition, the Newark Museum has a single stage 40 tadpole collected July 8, 1954, off U. S. Highway 301 south of Nahunta, Brantly County, Georgia. Despite the small amount of material, a number of additions to our knowledge of this form can be made.

Eggs; Ten eggs measured in early to middle cleavage stages have an average vitellus diameter of 0.95 mm., range 0.88-1.03. This is larger than the size given by Livezey and Wright (1947) which was 0.6-0.8 mm.; however, Wright (1932) mentioned "ripe ova" (apparently dissected from the ovaries of a 15.5 mm. female) as being 0.8-1.0 mm. In diameter of envelope, our sample has a mean of 1.57 mm., range 1.50-1.68, well within the range of 1.2-2.0, given by Livezey and Wright (1947). There is a single jelly envelope, its tenuous outer margin made visible mainly by the adhering bits of debris. Stages in embryonic development are similar to those of *H. regilla* as figured by Eakin (1947). The eggs hatched in about 3½ days at room temperature.

Larvae: The Nahunta, Georgia specimen previously mentioned is readily identified from Wright's (1932) description, but early stage tadpoles are rather different. Only those observations that supplement Wright's account are given here.

Three stage 20 hatchings average about 3.50 mm. in length, range 3.32-3.60. At stage 25 four larvae average 5.06 mm., range 4.70-5.35. Our material is inadequate to determine the size-staging curve for this species, but from the data available it is suspected that the curve for *ocularis* lies somewhat to the left of the curve for *Pseudacris nigrita feriarum* given by Gosner and Black (1957), indicating a smaller size in *ocularis*.

Adhesive organs are crescent shaped at stage 17 but bifid at

hatching. Nothing unusual was noted in their development compared to other eastern hylids known at present. The external gills are small and inconspicuous. The lower gill is the larger and has two subequal branches and a shorter branch below; the upper gill has a short lower branch.

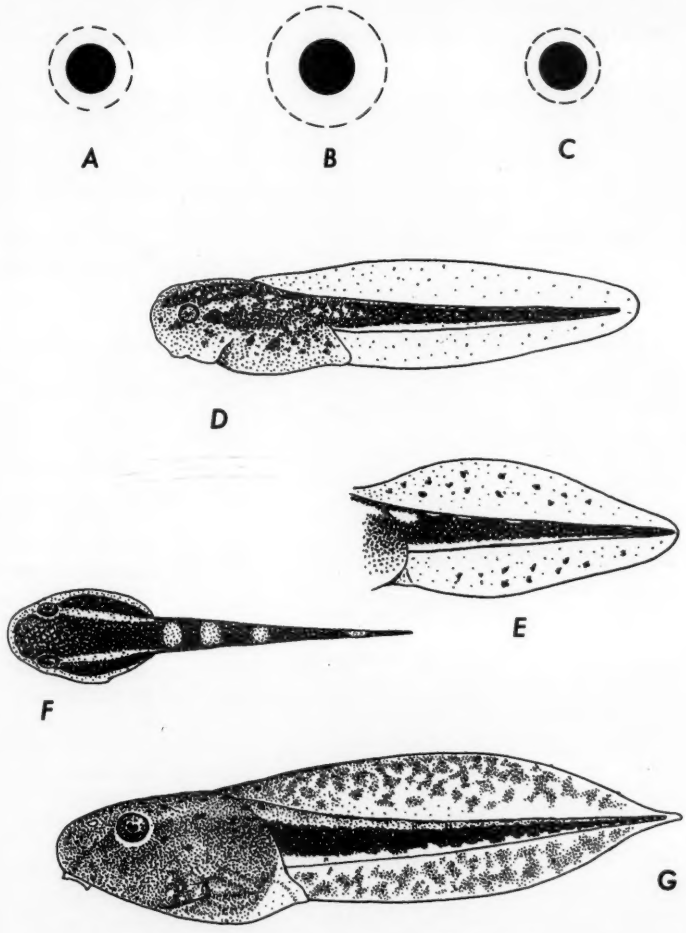

Fig. 1. Eggs of, A, *Hyla c. crucifer;* B, *H. c. bartramiana;* C, *H. ocularis;* D-G, *H. ocularis* larvae; D. larva, Stage 23; E, tail pigmentation and, F, dorsal aspect of early larva, Stage 28; G, mature larva at about Stage 35.

Hatchlings are light brown and cream colored. Beginning at stages 21-22 the tail is bicolored with a narrow light stripe on its ventral edge. By stage 23 formation of a light postocular stripe has begun; the tail musculature pattern at this stage is more sharply defined, with the light ventral stripe occupying one fourth or less of the lateral surface and narrowing still more basally (fig. 1). A series of six or fewer spots separated by wider dark areas appears at the same time. In life the light areas are a brilliant vermillion; this color persists for only a brief period, becoming golden yellow by about stage 28. The postocular light stripes are strongly defined and undergo a similar color change. These stripes extend backward from the eye and converge on the dorso-lateral part of the tail musculature anteriorly. Scattered dark flecks are present in the tail fins at stage 28.

Early larvae of *Pseudacris brimleyi* and *Acris gryllus*, species sympatric at least in part with *ocularis*, also develop reddish or orange-red pigmentation in the early larvae. Dark and light checks are more numerous on the tail musculature of *Acris*, however, while the tails of *brimleyi* tadpoles do not present a clearly checkered appearance. Parenthetically it may be noted that *Acris* tadpoles from the lower Coastal Plain of the Carolinas and Georgia, (*A. g. gryllus*), do not appear to differ from those found in New Jersey (*A. g. crepitans*), despite Orton's (1947) finding that Louisiana *gryllus* and *crepitans* larvae are separable, partly on the basis of checkered markings on the dorsal tail ridge. Initially the melanoid pigmentation of *ocularis* tadpoles is largely confined to deeper tissues. By about stages 36-37, changes in pigmentation appear, anticipating the condition described by Wright (1932). The darkly pigmented areas on the crest of the tail fade, leaving a light dorsal stripe with only faint traces of the original dark bars. At that stage the lateral surface of the tail has a broad straight-edged stripe which is very dark and conspicuous. The light stripe above is continuous with the postocular light stripes. The latter persist until obscured by an increase in surface pigmentation leading to metamorphic pattern changes. The dorsal surface of the head and body is flecked or stippled with golden yellow during mid-development; the over-all ground color appears olivaceous brown. The dark dorsal spotting reported by Wright does not appear in our specimens until about stages 45-47. The underside of the chest and throat, lightly stippled initially, becomes heavily flecked, blotched, or reticulated in older larvae. The underside of the hind legs is also heavily stippled, and the tibial dark stripes become strongly pigmented before transformation. Markings in the tail fins change from scattered specks to fairly heavy reticulations or blotches in a broad band down the middle of each fin. The distinctive markings and small size of the *ocularis* tadpole should provide a ready means of identification throughout the larval period;

as in North American hylids previously studied it is the pattern of the tail musculature that is most useful.

The following body ratios are based on Wright's (1932) published data plus the Nahunta specimen in the Newark Museum. By use of body length as divisor the following ratios are obtained: snout-spiracle 0.64-0.77, internasal 0.17-0.25, interocular 0.39, tail muscle depth 0.23, eye-snout 0.23-0.34, oral disc 0.23-0.25, total length 2.61-2.88 mm. Where only a single value is given above, the Nahunta specimen agrees with Wright's data; the ranges are not excessively broad when compared with those of other hylid tadpoles, except possibly the internasal and eye-snout ranges. This may be due in part to differences in measuring techniques. The only ratio of much interest as a possible diagnostic character is the interorbital ratio indicating a narrow head width in this species.

Details of oral disc structure were described by Wright (1932), but our Nahunta specimen differs in several ways from the published description. The papillary fringe is double and fairly even from above the first upper labial tooth row to just inside the edge of the third lower labial tooth row with a few extra papillae opposite the horny beak; Wright found some variation in this trait with papillae missing on the upper labium, opposite the horny beak, and below the second lower labial tooth row in some specimens. The gap between lateral elements of the second upper labial tooth row, described as 3-4 times the length of the row, is shown in Wright's figure to be much smaller than either lateral fragment; in our own specimen the gap is only slightly narrower. The horny beak was described as being about half the width of the first upper labial tooth row and the first and second lower labial tooth rows as being subequal, whereas in our specimen the second lower row is longer and the horny beak equals about 60 per cent of the first upper tooth row. Obviously further data are needed on variations in oral disc structures in this species. The following ratios are obtained from the Nahunta specimen using the first upper labial tooth row length as divisor: papillary-free gap on upper labium 0.56, second upper labial tooth row 0.39, gap between second upper labial tooth rows 0.33, horny beak 0.61, first lower labial tooth row 0.62, second lower labial tooth row 0.83, third lower labial tooth row 0.16.

Metamorphosis: The two specimens carried through metamorphosis underwent similar pattern changes. Prior to the appearance of the front limbs a dorsal pattern similar to that of the adult appears. Surface pigmentation gradually obliterates the larval postocular light stripes. The dorsal spots coalesce to form a dark middorsal stripe; a dark interorbital bar appears, plus a dark bar from eye to nostril, and a less sharply defined stripe extending posteriorly from eye through the angle of the jaw onto the flank. The tibial dark stripes are strongly defined. The larval period in the laboratory was about 42 days. Snout to vent length of the newly transformed frogs

was 7.8 mm. and 8.3; Wright (1932) gave the range as 7-9 mm. with the average between 8 and 9.

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NEWARK MUSEUM, 43 WASHINGTON STREET,
NEWARK, N.J., AND UNIVERSITY OF FLORIDA,
GAINESVILLE, FLA.

ERRATUM. In the paper "A New Subspecies of *Coniophanes fissidens* and Notes on Central American Amphibians and Reptiles," by Sherman A. Minton and Hobart M. Smith, Herpetologica, vol. 16, no. 2, 1960, p. 110, substitute the following for line 25:

Leptodeira annulata rhombifera Günther. A single specimen from the western edge of the city of San Salvador was found in a shallow pond and had eaten an *Euhemphix* and a *Hyla staufferi*.

Leptodeira septentrionalis ornata Bocourt x *L. s. polysticta* Günther. Golfito, C. R. The single specimen has some features of *ornata* (21 scale rows, 40 body blotches, compressed body), and of *polysticta* (3 preoculars), and is from a locality near an accepted area of intergradation that covers much of Costa Rica (Duellman, 1958, Bull. Amer. Mus. Nat. Hist., 114 (1):66, 70). Duellman (*op. cit.*:77) refers a single specimen from Puntarenas Prov. to *ornata*, numerous specimens from Cartago, Limón and San José provinces to intergrades, and a number from Limón province to *polysticta*.

Leptophis ahaetulla occidentalis (Günther). One adult found by

The Normal Daily Rhythm of Color Changes in the Lizard, *Anolis Carolinensis*, When Exposed to the Contrasting Background Color

CHARLES GORDON AND WADE FOX

The color changes in the "American Chameleon" or green anole are well known and have been utilized in several experimental studies. Rahn and Rosendale (1941) found that these lizards continued to exhibit a color cycle of brown during the day and green during the night even when placed in continuous darkness for 18 days. This paper presents data on the effects of background color on this diurnal rhythm.

MATERIALS AND METHODS

Between December 21, 1958 and March 30, 1959 thirty-three lizards of various sizes and of both sexes were captured in the vicinity of New Orleans, Louisiana. These were divided into three groups with a fairly even distribution of sizes, sexes and numbers of individuals. Nine to eleven individuals were kept in each group throughout this period. They were maintained in 3 cages of approximately the same size (6" x 8" x 10") that were lined with paper on two sides and the bottom. The other sides were covered with copper screen. One was lined with white paper, another with bright green paper and the third with black paper.

The cages were placed close together on the north side of the same room and exposed to the same conditions of temperature, humidity and light. The temperature of the room fluctuated between 70° and 79° F. Direct sunlight, not reaching the cages, entered the room on the east side in the morning only. The cages were sprayed with water daily and *Tenebrio molitor* larvae were supplied as food.

Observations were carried out over a period of two months. On certain week-ends records were made at half-hour intervals; otherwise records were made irregularly. The number of green and brown lizards in each cage was recorded at each observation. No distinction was made between bright green lizards and yellowish green lizards.

RESULTS

An examination of Fig. 1 reveals that lizards in all three cages tended to be uniformly green during the night except for some irregular fluctuations on the part of those in the cage with a black background during early evening. Animals in the cage with a white background were consistently the earliest to become 100 percent bright green in the evening. During the daylight hours many of the lizards were found to be brown. As shown in Fig.

1, the greatest number of brown animals were found in the cage with the black background. The difference observed between the lizards of the white-lined cage and those of the green-lined cage are relatively slight, but there appeared to be a stronger tendency toward brown skin color in the green cage than in the white cage. Whereas 55-90% of the lizards in the black cage tended toward brown, only 17-40% turned brown in the cages with the lighter backgrounds.

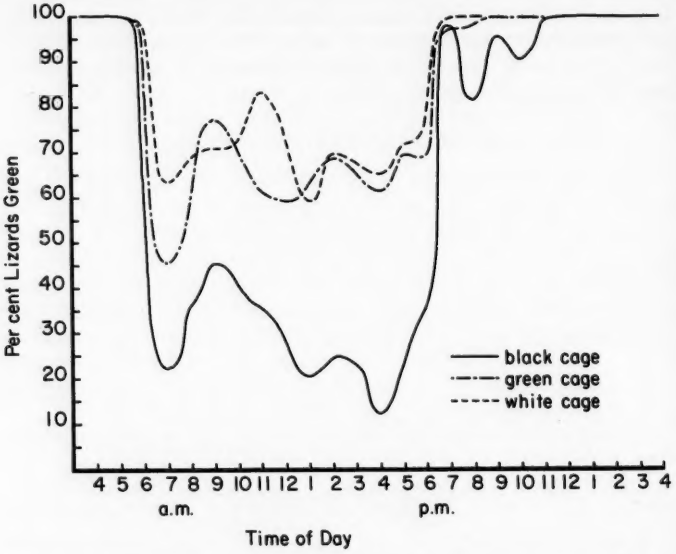

Fig. 1. Average daily color rhythm of green anoles maintained in cages with black, green, and white linings. All lizards were green during the night; a greater percentage of lizards was brown during the daylight in the black-lined cage.

DISCUSSION

In these experiments the tendency for anoles to turn green at night and brown during the daylight is verified. However, background color has a significant effect in the determination of skin color during the daylight. More than half of the lizards were classified as green in the cages with bright green or white backgrounds and 55 to 90 percent were classified as brown in cages with black background. It is significant that during the daylight hours the skin colors were never completely correlated with background color.

These experiments did not take into account the possible effects of temperature on the skin color of the lizards. Observations on wild animals during the heat of summer suggest that all anoles are green during the daylight, at least while the typical temperatures of 80-90° F prevail. Even in the spring when day temperatures may only climb to the 70's most of the wild lizards observed around mid-day are green. In addition, these animals are found to be green when on dark brown or gray backgrounds as well as on green leaves. However, in the cooler parts of the day in the spring, fall and winter most animals are observed to be brown. The usual interpretation of this observation is that the brown skin color absorbs more radiation and enables the animals to achieve temperatures considerably higher than the air temperature. Conversely when they have reached a sufficiently high body temperature the green color would be advantageous in reflecting much of the radiation and thereby preventing excessive heating. One further common observation on natural color selection by anoles is that nearly all lizards found in their open, nocturnal roosts are in the green color phase. Only infrequently are brown lizards found in the open at night.

Considering our observations on both wild and captive anoles it would appear that temperature plays a major role in control of skin color of these animals. Within certain temperature ranges there appears to be a marked diurnal rhythm of brown during the day and green during the night. Further, at moderate temperatures the preference for brown during the day is significantly altered by background color.

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BENJAMIN FRANKLIN HIGH SCHOOL AND LOUISIANA STATE UNIVERSITY SCHOOL OF MEDICINE, NEW ORLEANS, LOUISIANA

Sceloporus p. poinsetti taken in Sonora.—On May 30, 1956, a subadult male (BYU 13491) was taken 4 mi. E of Nutria Ridge which is approximately 20 mi. W. of the Sonora-Chilmahua line and near the point where the Rio Bavispe flows into Sonora.

The present specimen definitely establishes this species in Sonora as was suspected by Bogart and Oliver (1945, Bull. Amer. Mus. Nat. Hist., 83:412)—Wilmer W. Tanner, Brigham Young University, Provo, Utah.

THE SCIENTIFIC NAME OF THE RED-BACKED SALAMANDER.—In a recent issue of this journal, Reed (1960, Herpetologica, 16: 207-13) called attention to the fact that the specific name of the red-backed salamander, now known as *Plethodon cinereus*. (Green, 1818), is a junior synonym of a name proposed by Rafinesque six months before Green's description of *Salamandra cinerea*. Under the application of the law of priority, the scientific name of the red-backed salamander would be changed to *Plethodon erythronotus* (Rafinesque, 1818).

The combination *Plethodon cinereus* has been used by most zoologists who correctly recognized that the striped and unstriped color phases of this common salamander were conspecific since Tschudi erected the genus *Plethodon* in 1838. Stejneger and Barbour (1917, A Check List of North American Amphibians and Reptiles: 15) considered Tschudi to be the first revisor, who chose the name *cinereus* rather than *erythronotus* for the species. During the 19th Century and the early portion of the 20th Century, the two color phases were often regarded as distinct species and thus the name *Plethodon erythronotus*, incorrectly attributed to Green, was commonly used. However, even during this period, in spite of the fact that the striped phase is more common over much of the range of the species, the combination *Plethodon cinereus* was more frequently cited.

Because of the long usage of the combination *Plethodon cinereus*, first proposed by Tschudi in 1838, and the almost exclusive use of this combination during this century by zoologists who correctly recognized that the red-backed and lead-backed phases were conspecific, as well as the fact that the scientific name of this animal is very well known in the literature of vertebrate zoology and the popular literature, a change in the name would result in tremendous confusion. An application to the International Commission on Zoological Nomenclature was submitted on September 26, 1960, to propose that the Commission use its plenary powers to suppress the name *erythronota* Rafinesque and to place the specific name *cinerea* Green, 1818, as published in the combination *Salamandra cinerea*, on the Official List of Specific Names in Zoology.

Under the International Rules of Zoological Nomenclature, while a case is before the Commission for consideration, there should be no change in the current use of the name. Therefore the red-backed salamander should continue to be known by the scientific name *Plethodon cinereus* until the final decision by the International Commission on Zoological Nomenclature.—*Richard Highton, Department of Zoology, University of Maryland, College Park, Maryland.*

Breeding and Growth in Woodhouse's Toad

JAMES C. UNDERHILL

One of the more common amphibians of the floodplain of the Missouri River in southeastern South Dakota is Woodhouse's toad, *Bufo w. woodhousei* Girard. An intensive survey of the southeastern portion of the state has revealed that Woodhouse's toad is largely restricted to the floodplain habitat and is rarely found on the neighboring uplands. The latter habitat is occupied by *B. cognatus* and *Scaphiopus bombifrons* (Underhill 1958, Fishbeck and Underhill 1960); these species have been taken only four times in the floodplain. Wright and Wright (1949) and Stebbins (1954) have discussed the taxonomic status and biology of *B. woodhousei*, and Bragg (1940) has treated the breeding and growth of the species in Oklahoma.

Large breeding populations of Woodhouse's toad were found in the backwaters of the Missouri River. Calling during the peak of the breeding season, early May, was deafening. The large numbers of toads and the ease of access to the floodplain suggested the possibility of carrying out growth studies. The primary study area selected was a large sand dune southwest of Elk Point, Union County, South Dakota. Three other stations were utilized to a lesser extent: a sand dune two miles south of Vermillion, a sand bar seven miles west of Vermillion, and several sand bars below the Gavin's Point Dam west of Yankton, South Dakota. In each of the areas there were numerous small ponds, some permanent, but many were temporary and dependent on the water released from the upstream impoundments.

Males of *B. woodhousei* were the first to appear in the breeding ponds, usually a week to ten days before the females began entering the ponds. In 1957 the first calling males were heard April 4, but the first eggs were not collected until April 30. Low temperatures at night apparently inhibited the males from calling for two nights in a row and may have caused the unusual delay in breeding. Dry weather may also have been a contributing factor. Breeding in 1957 continued until May 28. Breeding pairs and eggs were first collected on April 14 in 1958 and breeding continued into late May. In 1959 the first breeding pairs appeared on April 25; the late appearance of toads was again associated with an abnormally dry spring. Bragg (*loc. cit.*) has pointed out that breeding may occur in the absence of spring rains but that large aggregations are more usual following the first warm rains of spring. Early and late breeders selected quite different ponds; the early breeders generally selected the shallow smaller ponds, while the late breeders used the larger ponds and ox-bow lakes. In late April and early May the latter habitats were cold and little influenced by the daytime

temperature, while the water in the smaller ponds had tempratures as high as 85° F. by late afternoon. In many instances the smaller pools and ponds were dry before the toad tadpoles had completed their development, so that the early breeders left fewer offspring than did those pairs which bred in permanent ponds in middle and late May. The latter phenomenon may be the result of fluctuating water levels associated with the multiple purpose Missouri River impoundments and may not have been too important in the pre-impoundment period when the entire floodplain was covered with water during the spring months. In the years 1956 through 1959 breeding was completed by the end of May.

The minimum size for breeding males was 55.8 mm. from the tip of the snout to the vent, while the smallest female was 67.3 mm. in length. The size distribution of males and females during the breeding season (late April and May) at Elk Point, South Dakota, is presented in Table 1. Sampling at other stations and in other years revealed similar size class distributions. The number of females in the samples were smaller than the number of males because of behavioral differences between the sexes. The males called and were easily located; they also remained in or near the breeding ponds for long periods of time. Females generally entered the ponds in the early evening and had left by dawn, although on several occasions pairs were taken in amplexus in the early daylight hours. Males were common in the ponds during the day but remained hidden in the previous year's growth of *Typha*. In contrast, females were found under driftwood on the sand dune away from the pond margin or back in the willow thickets bordering the ponds.

Few predators were in evidence during the breeding period,

Length in Snout-Vent	April-May			June			July			August			Total
mm.	?	♀	♂	?	♀	♂	?	♀	♂	?	♀	♂	
10 - 19.9				155									155
20 - 29.9				15	1		77		1	16		1	111
30 - 39.9					8	7	31	7	6	40	9	9	117
40 - 49.9					24	43	1	2	4	1	5	6	86
50 - 59.9			6		6	9			1		3	3	28
60 - 69.9		3	25			5						1	34
70 - 79.9		5	24		2	1							32
80 - 89.9		7	2		3								12
90 - 99.9		2			1								3

Table 1. Snout-vent lengths of Woodhouse's toads taken during April-August, 1959, from the sand dunes at Elk Point, South Dakota.

but on four occasions the dismembered bodies of toads were found. Most of the body was missing in most cases, but the parotoid glands were always undisturbed and usually a large portion of the dorsal skin. One morning while I was observing the behavior of *Pseudacris nigrita* on the pond south of Vermillion, a great blue heron flew into the pond. The heron stalked slowly along the margin and then struck at something, but the object could not be discerned. Shortly the bird was disturbed and flew off, and I walked over to where it had been and found the remains of a male toad. On the other occasions when toad remains were found, an American Bittern had been feeding on the pond and a migrating flock of night herons had been seen in the *Typha* on the pond margin. It seems doubtful that mammals were responsible, and while the evidence is circumstantial, birds appeared to be the predators. All the toads that could be sexed were males. As many as twenty carcasses were found in the breeding pond south of Vermillion. The two principal reptilian predators on Woodhouse's toad, the eastern hognose, *Heterodon platyrhinos*, and the common garter snake, *Thamnophis sirtalis*, were not active until early June and were never observed in or near the breeding ponds until the newly metamorphosed toads appeared.

The first newly metamorphosed toads appeared on June 19 in 1958 and 1959. Large numbers of young toads were not taken until the last week in June. Tadpoles of Woodhouse's toad were in evidence in the ponds as late as the middle of July. The long period during which newly metamorphized toads appeared introduced an unforeseen complication in the computation of growth rates, as certain toads had what was the equivalent of a half year's growth before the other members of the same year class had completed their metamorphosis.

The size of toads taken during the period April through August in 1959 is presented in Table 1. Young newly metamorphosed toads approximately 10 mm. in snout-vent length had an average weight of 0.1 gram. This is in contrast to the size of newly metamorphosed toads in Oklahoma which averaged 12.7 mm. in length (Bragg 1940). By the end of July toads which had metamorphosed in June had an average length of 27.3 mm. and a weight of 2.9 grams, and by late August their lengths averaged 31.5 mm. and their weights 5.4 grams. Individuals taken in June having lengths between 25 mm. and 50 mm. represented toads of the 1958 year class. The fact that no toads smaller than 50 mm. were taken during the breeding season indicates that toads in South Dakota do not mature until age two, i.e. the second summer of life. Perhaps females may not mature until the third year of life. In South Dakota it takes Woodhouse's toad two years to reach the same length that Oklahoma individuals reach by October of their first year of life (Bragg 1940).

The study of growth in larger specimens was based on in-

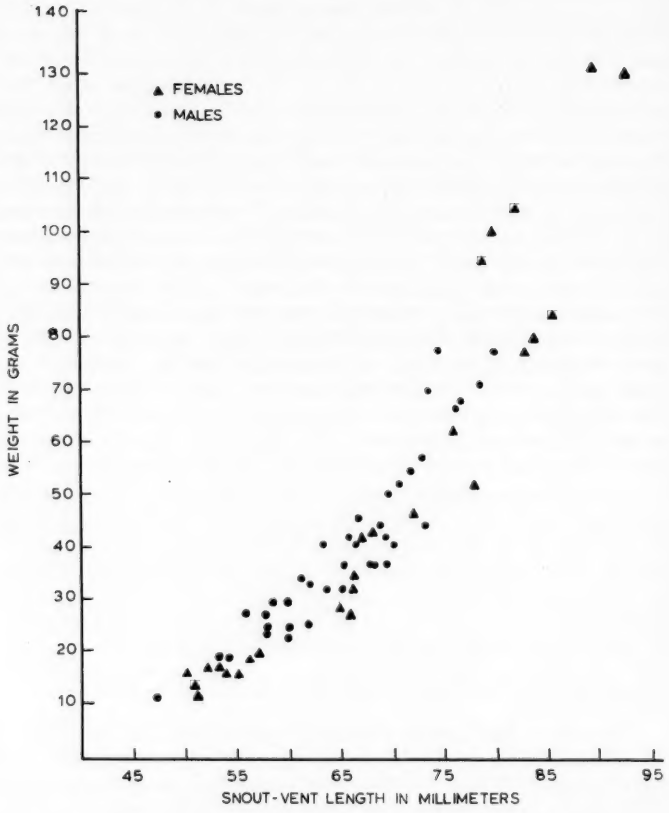

Figure 1. Lengths and weights of *Bufo woodhousi* from Elk Point, South Dakota.

dividuals that were returned to the laboratory and preserved for studies on variation in addition to specimens that were marked and returned to the sand dune area. In Fig. 1 the lengths and weights of toads over 45 mm. in snout-vent length have been plotted. In the growth study toads were collected in canvas bags, brought into the laboratory and held for twelve hours. They were then measured, marked, returned to the sand dune and released. Holding the toads for twelve hours assured that any food they had recently ingested would be digested before they were weighed. Some of the vari-

ability encountered in preliminary studies was a result of the amount of food that had been ingested by the toad just prior to its capture. After twelve hours most of the indigestible chitinous material had been defecated. Small toads were grouped by size classes, weighed and the average weight computed from the aggregate weight. Larger specimens were weighed individually to the nearest 0.1 gram and measured to the nearest 0.5 mm. and an estimate to the nearest 0.1 mm. was made. Toads were marked by toe clipping following the method outlined by Martof (1956).

During the summer of 1959, 263 toads were marked, and of these only twenty or 7.6 percent were recaptured. The results, while disappointing, did provide some information about growth in *B. woodhousei*. Individuals marked and recaptured 4 to 9 days following release lost up to 6.7 grams, indicating that toe clipping may have had an adverse effect on the toads' normal feeding behavior. Therefore the values for weight gains based on marked individuals are probably low. Only two individuals were recaptured twice; toad number 14 was marked June 12, recaptured June 18 and had lost 1.0 gram but when retaken June 21 had regained the loss plus 1.2 grams. Toad number 162, captured July 21 and recaptured 9 days following the marking had lost 0.9 grams but 18 days later had made up the lost weight plus 12.7 grams. Weight gains, increases in length and their ratios were quite variable, and while there appeared to be no relationship between gains and size at capture or time of year, with such a small sample it would be unwise to generalize. For example, toad number 7 weighed 8.8 grams when captured and 49 days later when recaptured weighed 25.0 grams; in this period it increased in length from 40 mm. to 56 mm. The latter example is representative of the increases in length and weight

Sex	N		Range	Mean	Correlation Coefficient
Male	65	Length	37.0 - 84.0	62.2±1.05	0.921
		Weight	7.5 - 78.0	44.5±2.1	
Female	34	Length	29.2 - 92.8	63.6±3.2	0.890
		Weight	3.8 -158.0	43.3±7.4	
?	195	Length	10.0 - 40.0	29.4±0.42	0.855
		Weight	0.1 - 10.6	3.9±0.16	

Table 2. Average length in millimeters and weight in grams of *B. woodhousei* from southeastern South Dakota.

of six other toads recaptured 29 days after they were marked; each showed an increase of at least 1 gram in weight for each millimeter increase in length.

The means, standard errors and correlation coefficients of body length and weight were calculated for males, females and toads up to 40 mm. in length that could not be sexed externally (Table 2). The difference between the correlation coefficients for males and females, with z values equal to 1.59 and 1.42 respectively, is not significant ($p = 0.25$). The following equations may be used to estimate body weight (X) from the body length (Y) of *B. woodhousei* from southeastern South Dakota.

Males	$X = 1.84Y - 77.0$
Females	$X = 2.07Y - 85.6$
Sex ?	$X = 0.32Y - 5.5$

I wish to express my sincere appreciation to Donald Fanslow and Dale Fishbeck for their assistance in much of the field work, and to William Nelson for help in preparing Figure 1. A grant-in-aid from the research fund of the State University of South Dakota made the field work possible.

SUMMARY

Bufo woodhousei breeds in late April and May in southeastern South Dakota. Newly metamorphosed toads 10 mm. in length and weighing 0.1 grams first appeared on June 19 in 1958 and 1959. Young of the year were 27.3 mm. long, weighed 2.9 grams by late July, and by late August reached a length of 31.5 mm. and a weight of 5.4 grams. The growth rate of South Dakota toads is only approximately half that reported for toads from Oklahoma.

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Geographic Variation of *Bufo spinulosus* in Chile

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Introduction

Bufo spinulosus Wiegmann occupies an extensive area reaching from the northern Andean highlands of Peru to the cold southern rainforests of Chile (Province of Chiloe). On the western slopes of the Cordillera, it is found from an elevation of 4,500 meters to the seashore. On the eastern slopes of the Andes, it is only found above 1,200 meters. In Chile this toad is the most adaptive and predominant form, inhabiting almost all of the possible ecological niches. Five well-defined geographical forms were recognized by Vellard (1959) in Peru. The description and interrelation of the numerous Chilean populations of this polymorphic toad and their geographical distribution is the purpose of the present paper.

Material and Methods

All of the studied samples were observed and measured alive in the field in 1957, with the exception of Valdivian specimens collected in 1952 and preserved in a mixture of alcohol and formalin. Color descriptions are based entirely on living specimens. The characters analyzed are those appearing in the generally accepted diagnoses of the species (Wiegmann, 1834; Boulenger, 1882). Sexual maturity was determined according to the criteria cited by Inger (1954:203). Measurements were taken with calipers and are accurate to 0.5 mm. The standard error was calculated for the various measurements, and the Student's t test and the tables of Fisher and Yates (1948) were used.

The following measurements were made: snout-vent length; head width taken between centers of tympana; head length from tip of snout to line joining centers of tympana; hind leg length from tip of fourth toe to groin; fore leg length, from tip of third finger to axilla; distance from tip of snout to nostril; distance from nostril to eye; interorbital width; width of upper eyelid; snout length, from tip of snout to interorbital axis; parotoid diameter.

Samples were examined from the following localities (Fig. 1):

1. Puna de Atacama, E. of San Pedro de Atacama, Prov. of Antofagasta; under stones and rocks, along the little streams of the mountains (Arroyo Bilema) above 2500 meters (July, 1957): *19*[1], *413, 414* (Fig. 2).
2. Paposo (Quebrada de Caleta Paposo). Prov. of Antofagasta; under stones and in water, in little streams, near the Pacific

[1]Italicized numbers refer to collections of the Centro Investigaciones Zoologicas (C.I.Z.) of the University of Chile, Santiago, in which some samples are deposited.

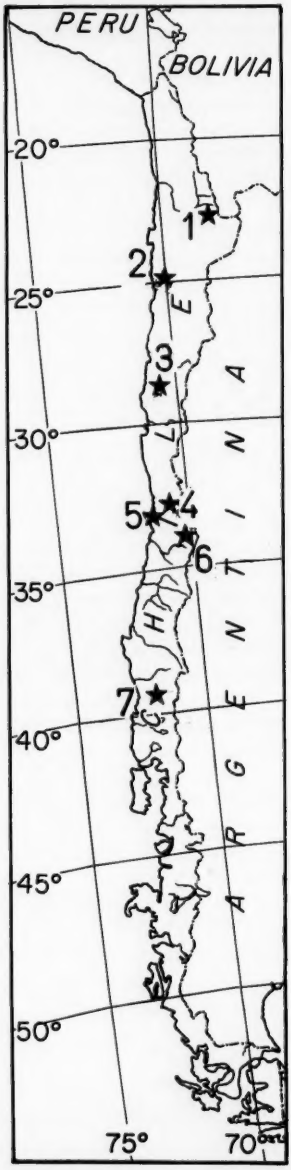

Fig. 1. Map of Chile showing the seven populations studied: 1. Puna de Atacama, 2. Paposo, 3. Vallenar, 4. Santiago de Chile, 5. Casablanca, 6. Central Cordillera, 7. Valdivian Lakes.

Coast, a few hundred meters above sea level (July, 1957): *18*.

3. Vallenar, Prov. of Atacama; under stones in Huasco River, near the town, 380 meters (July, 1957): *131*, (Fig. 2).
4. Santiago de Chile, Potrerillo, near Nilhué Bridge, 800 meters (September, 1957).
5. Casablanca, Curacaví Valley, S. E. of Valparaiso, arid coast zone, 300 meters (Aug., 1957).
6. Central Cordilleras, E. of Santiago, lo Valdés, above 1500 meters (Sept., 1957): *415*, (Fig. 2).
7. Valdivian Lakes, Prov. of Valdivia, near Enco and Caburgua (Summer, 1952): *54, 185*, (Fig. 2).

Of the 245 toads analyzed statistically, 106 were males, 88 females, and 51 unsexed juveniles. Observations made on 132 additional specimens from Chilean localities were not statistically considered: Putre, in Tarapacá mountains; Puna de Atacama; Loa River, N.W. of Calama; Copiapo, Prov. of Atacama; Talinay, Prov. of Coquimbo; Zapallar, N. of Valparaiso; Baño Morales, Central Cordilleras, Santiago, 2500 meters; Talca; Concepción; Angol. Prov. of Malleco; Valdivian Lakes.

Four geographic groups of Chilean populations are represented: (1) the toads from the northern arid mountains of Puna de Atacama; (2) the isolated populations of the rivers and streams of the Atacama Desert (Paposo and Vallenar); (3) the central Chilean populations of the xeric region of the *Acacia caven* steppe as far as the western Andean slope (Santiago, Casablanca, and Cordillera Central); and (4) the toads of the cold Valdivian rainforest of the extreme south. The ecological circumstances of each group are distinctive.

Analysis of Variation

Ranges and means and their standard errors of the eight measurements were calculated. Comparisons between each pair of samples were made for all eight measurements, considering sexes separately. In Table 1 statistically significant differences (P equal to or less than 0.05) are indicated by a plus sign, while a negative sign indicated comparisons that were not significantly different.

Sex dimorphism in the characters listed in Table 1 reached statistically significant levels in the Puna de Atacama sample (size, head shape, relative hind leg length, and nostril position), in the Cordillera Central sample (head shape and interorbital), and in the Valdivia sample (size).

Besides the characters listed in Table 1, the following also serve to distinguish the various populations:

1. When the hind limb is brought forward, the tibio-tarsal articulation usually (*i.e.*, 50 per cent or more of toads examined)

reaches the parotoids or beyond, but in 75 to 100 per cent of both sexes from Santiago and of females from Casablanca and Valdivia, that joint reaches only as far as the shoulder.

2. Very rough, warty skin characterizes toads from Puna de Atacama and the Cordillera Central, and both groups produce an irritating, sticky, and aromatic secretion. The skin in the remaining samples is relatively smooth (especially in Paposo-Vallenar toads) with rounded tubercles and produces very little secretion, which is usually odorless.

3. The roughness of the skin is carried over to the parotoids, which are granulate and warty in the Puna de Atacama toads. In other populations the parotoids are rather smooth, though porous. These glands are rounded in outline except for the subtriangular shape in Vallenar toads.

4. The general ground color of the dorsum is yellowish or olive brown over which irregular large dark spots are usually scattered. The spots are smaller and less frequent in occurrence in the Puna de Atacama, Cordillera Central, and Valdivia toads (Fig. 2). Ventrally all samples are whitish, usually immaculate, or with a few small dark spots. However, the Valdivian toads have a bold, black reticulation covering the entire ventral surface.

5. Juveniles from Paposo and Copiapó are brownish or grayish above with brilliant red color on the tubercles, parotoids, and upper eyelids. Their plantar surfaces are yellow or orange. Juveniles of other populations resemble the corresponding adults.

6. A "hypnotic" defensive reflex similar to that described for *Bufo arenarum* (Cei, 1956 and 1959) occurs in *spinulosus* and varies in frequency of expression as follows: Puna de Atacama, 0 per cent of individuals tested; Paposo 5.2 per cent; Vallenar 22.9 per cent; Santiago 17.2 per cent; Casablanca 66.0 per cent; Cordillera Central 0 per cent. No living Valdivian toads were available.

Discussion

The small, warty toads of Puna de Atacama differ from the populations to the south and southwest in most of the characters listed in Table 1 and in the roughness of the skin. The barrier formed by the great Atacama Desert to the south probably accounts for this differentiation. It is interesting that the Puna de Acama toads do not differ from those from the north (Putre, Chile, and Cuzco, Peru). Either the conditions of selection are much the same from Puna de Atacama to Cuzco, or dispersal is relatively easy in this mountainous area, or both.

The second Chilean group, from the areas of Paposo and Vallenar, are partially isolated by desert from populations to the north and south. They are larger and smoother than Puna de Atacama

toads, but not so large as those from central Chile. In general, they are intermediate between those two groups of populations and less differentiated than Puna de Atacama toads.

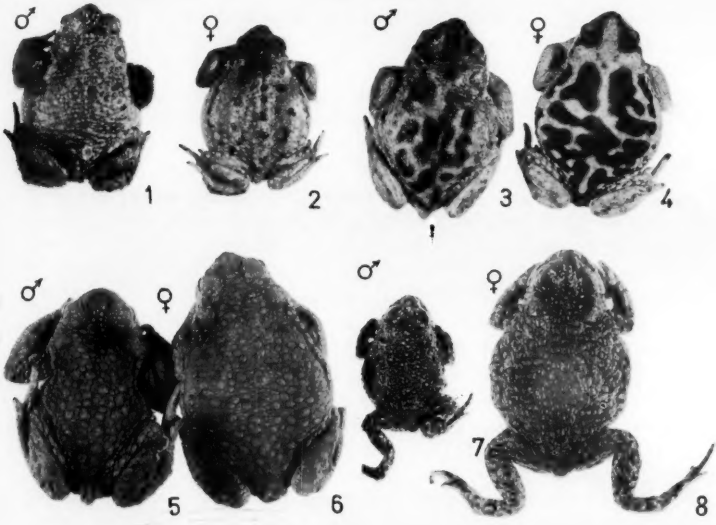

Fig. 2. Dorsal views of male and female specimens of *Bufo spinulosus* from the four geographic groups studied: 1-2 Puna de Atacama, 3-4 Atacama Desert, 5-6 Central population (Cordillera), 7-8 Valdivia.

The central Chilean populations, from Santiago, Casablanca, Cordillera Central, Valparaiso, and Coquimbo, attain the largest size of any Chilean toads. Their legs are somewhat shorter than those of toads to the north.

The fourth group of populations, from the Valdivian rainforest, is the only one in Chile occupying a truly humid zone. Next to the Puna de Atacama group, these toads are the most differentiated of the Chilean populations. The small size and the boldly marked venter are especially conspicuous. A related species, *Bufo variegatus* (Günther), is sympatric with *spinulosus* in this southern forest region.

Local differentiation among the Chilean populations of *spinulosus* are most pronounced at the extreme north and south. In the north, the desert, a barrier to dispersal, presumably has permitted Puna de Atacama toads to acquire local characteristics. In the south

Table 1. Statistically significant (+) difference between samples of *Bufo spinulosus* in characters of Table 1.

Populations	Sex	Snout-vent	Head shape	Hind leg	Fore leg	Interorbital	Nostril position	Snout: Interorbital	Parotoid	Total sig. diff.
Puna de Atacama — Paposo	♂	+	o	+	+	+	+	+	+	7
	♀	+	o	+	+	+	o	+	o	5
— Vallenar	♂	+	+	+	+	+	+	+	o	7
— Santiago	♂	+	+	+	+	+	+	+	+	8
	♀	+	+	+	+	+	+	+	o	7
— Cordillera	♂	+	+	o	o	+	+	+	o	5
	♀	+	o	o	+	+	+	+	o	5
— Casablanca	♀	+	o	o	+	+	+	+	o	5
— Valdivia	♂	+	o	o	+	+	+	+	+	6
	♀	o	o	+	+	+	o	+	+	5
Paposo — Vallenar	♂	o	o	+	o	+	o	o	o	2
— Santiago	♂	+	o	o	+	+	+	o	o	4
	♀	o	o	o	o	o	o	o	o	0
— Cordillera	♂	+	+	+	o	o	o	o	o	3
	♀	o	o	+	o	o	+	o	o	2
— Casablanca	♀	+	o	+	o	o	+	o	o	3
— Valdivia	♂	+	+	+	+	+	o	o	o	5
	♀	+	o	o	o	o	+	o	o	2
Vallenar — Santiago	♂	+	o	+	+	+	+	o	o	5
— Cordillera	♂	+	+	+	o	+	o	o	o	4
— Valdivia	♂	+	+	o	+	+	o	+	o	5
Santiago — Casablanca	♀	o	+	o	o	o	o	o	o	1
— Cordillera	♂	+	+	+	+	+	o	o	o	5
	♀	o	+	+	+	o	o	o	o	3
— Valdivia	♂	+	+	+	o	+	+	+	o	6
	♀	+	o	o	o	o	+	o	o	2
Casablanca — Cordillera	♀	o	o	o	o	+	o	o	o	1
Cordillera — Valdivia	♂	+	+	o	+	o	o	o	+	4
	♀	+	o	+	o	o	+	o	o	3
Casablanca — Valdivia	♀	+	o	o	o	o	+	o	o	2

no such barrier exists, but the radically different conditions of selection to be found in humid forest as compared to steppes may account for the differentiation of the Valdivian toads. Supporting the last suggestion is the striking morphological parallelism of Valdivian *Bufo variegatus* with the local population of *B. spinulosus*.

Brown (1957) has called attention to a common phenomenon of speciation in which distinct races and daughter species accumulate at the periphery of the range of a species. Brown designates this phenomenon "centrifugal speciation" because he considers the center or main body of the species population to be the principal source of evolutionary change and suggests that variants radiate from the center to become isolated or semi-isolated at the periphery during unfavorable periods of range contraction. *Bufo spinulosus* and its relatives may be a case in point. A similar interpretation of geographic variation can be applied to another widespread Chilean species. *Pleurodema bibroni* (Cei, 1959a), and to the occurrence of oviducts in male *Rana pipiens* (Moore, 1944).

As we have just seen, local differentiation of *spinulosus* is best developed at the extreme north and south of its range in Chile. Vellard (1956) suggests that *Bufo trifolium* or *cophotis* in the north and *Bufo variegatus* in the south occur with *spinulosus* as distinct but closely related species. If *cophotis* and *variegatus* are in fact derived from an ancient *spinulosus*-like stock, they represent earlier waves of emigration from the center of the range and have developed isolating mechanisms while in these peripheral situations. When subsequent waves of emigration reached these areas, hybridization either was restricted or did not occur because isolating mechanisms had developed in the intervening time. The types of *spinulosus* characteristic of the Puna de Atacama and the Valdivia populations represent these later emigrations, and presumably are themselves now acquiring the characters leading to reproductive isolation.

Summary

Analysis of geographic variation shows that populations of *Bufo spinulosus* Wiegmann are differentiated in Chile. Four recognizable, though broadly intergrading, population groups are indicated, corresponding to: (1) the northern mountainous arid environment of the Pune de Atacama plateau; (2) the isolated valleys and streams of the desert area of Atacama; (3) the central area between Coquimbo and Angol; and (4) the southern, humid Valdivian Forest.

Polymorphism was observed in some characters and clinal tendencies in others.

Acknowledgments

I wish to thank Dr. R. F. Inger of the Chicago Natural History Museum and Dr. Rodolfo Ruibal of the University of California,

Riverside, for their very valuable criticism and help. I am also indebted to the late Dr. K. P. Schmidt for many friendly suggestions.

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Notes on the Breeding Biology of the Red-Legged Frog (*Rana aurora aurora*)

ROBERT M. STORM

Little has been published concerning the various phases of reproduction in the red-legged frog *Rana a. aurora*. The author has accumulated material on these phases over a period of several years, assisted in part by grants from the General Research Fund of Oregon State College. The majority of the data was accumulated in the vicinity of Corvallis, Oregon.

This subspecies ranges "from southwestern British Columbia south in coastal regions through Washington and Oregon into northwestern California–." (Stebbins, 1951). It has been found in western Oregon from sea level to 3800 feet on the west flank of the Cascades (Dunlap, 1955). Of 121 non-breeding specimens in the Oregon State College collection, for which habitat information is available, 95 (78.5%) were collected in the water and the remainder were taken within a few feet of it. Frogs often forage in damp well-shaded areas during the day and are active during warm rains at night. More night collecting would undoubtedly show a greater departure from aquatic surroundings.

In the central Willamette Valley of western Oregon, waters utilized for egg-laying must fulfill a certain few requirements, which can be simply stated as follows: little or no flow; presence of water until at least early June; depths of 5 to 6 inches or more; and the presence of fairly sturdy underwater supports such as slender willow stems or branches, cattails, submerged weed stems, or aquatic plants. Three favored breeding areas have been known to be well-utilized in the past. Number one is located 12 miles south of Corvallis, and is locally known as McFadden's Marsh. This is largely a shallow marsh, 20 to 30 acres in extent, produced by the damming of Muddy Creek. The normal average depth is between 2 and 3 feet, and the marsh supports a heavy growth of submerged aquatic plants, largely water smartweed and water celery. Emergent sedges and spikerush are common, and large patches of the shrub *Spirea* grow in the water. A favored site of egg deposition is over 4 or 5 acres at the east edge of the marsh, where the water averages 12 to 15 inches deep, the eggs being attached to underwater stems of sedges, water celery, and *Spirea*. There is a slight current here during times of higher water, and the eggs are usually found on the downstream side of sedge or *Spirea* clumps. On March 17, 1951, 75 egg masses were in an area about 400 by 50 yards. The second site (now destroyed by drainage operations) was a small backwater of Bull Run Creek at a point where it crosses the Bellfountain Road some 6 miles south and

west of Corvallis. This was a small triangular area about 100 by 70 by 40 feet in dimensions and up to 3 feet deep in the early spring. It supported a heavy growth of cattails which were present as the previous year's dead growth during breeding time. Several willows grew in the water at the west edge. On March 17, 1951, 48 egg clumps were counted here, most being attached to cattail spikes

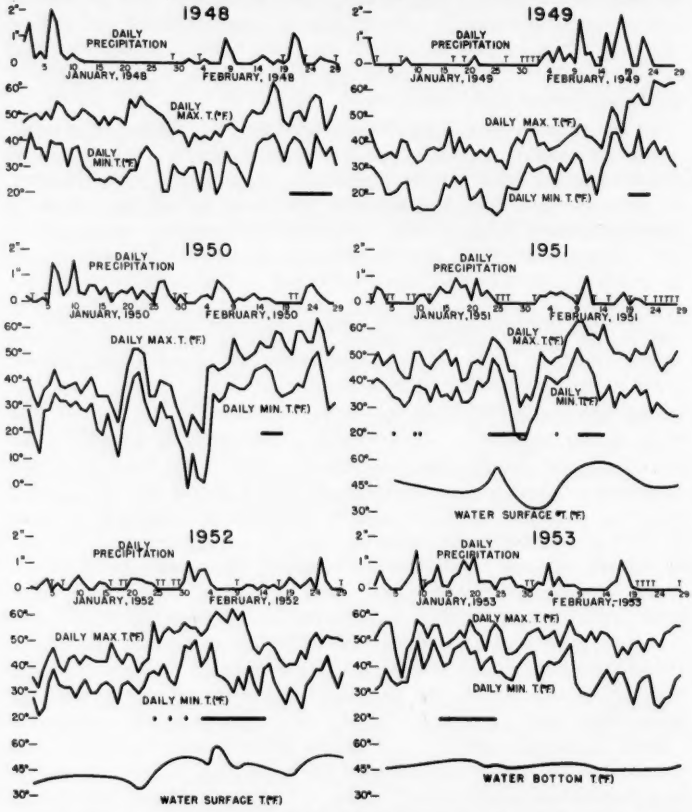

Figure 1. A summarization of six years of observations as they relate to climatic data, including water temperatures from 1948 to 1953. The solid horizontal bars in each year indicate *aurora* activity. Heavy dots at the same level indicate one or two specimens, hence minor observations. Daily precipitation records and temperature minima and maxima are based on Corvallis weather bureau records, which have been corrected by a factor to allow for the fact that the weather station is at a somewhat higher elevation.

or willow stems, with one having been placed on a strand of an old wire fence which traversed the pond. A third breeding area is a temporary pond, located one mile west of Corvallis. This pond has been the site of a special four-year study, discussed elsewhere (Storm and Pimentel, 1954). It is approximately .7 acre in extent, with a maximum depth of about 3 feet. It is approximately 150 feet from a small permanent creek and is surrounded by pasture. The pond becomes dry during late May or June each year, and during the dry season, mesophytic weeds grow in the pond area. It is to the dead stems of these weeds that a few *Rana aurora* attach their eggs each year. A more thorough discussion of this pond will be given below.

Breeding Migrations: Movement to the breeding areas is closely related to weather conditions occurring after approximately January 1.

It is apparent from Fig. 1 that after January 1 frogs are stimulated to move to breeding areas when air temperatures of about 50° F., or above, are accompanied by moderate to heavy rains. Once breeding activity starts, it becomes intensive, so that the total period of such activity in any one year in a given area tends to be short, perhaps not more than two weeks. Information on routes of travel to the breeding ponds is inconclusive. It is evident from highway cruising during favorable nights in February that frogs travel overland; however, there is no reliable evidence that such frogs are directed toward a specific pond. There is some evidence that they merely move to water, whereupon other factors may guide them. At the McFadden location, water would frequently overflow a road traversing the marsh during heavy rains. Both sides of the road were built up to some extent by rock rip-rap, and relatively quiet water prevailed in the lee of the downstream rocks. Here, on February 8, 1951, eight males were seen resting at the surface in quiet water, and two amplectic pairs were seen on the bottom adjacent to the rocks. It may be assumed that the frogs drift with the current until a suitably quiet area is reached. At the Bull Run Creek locale (see above), the creek flows past the opening of the small slough, and it seems possible that frogs can drift with the current until opposite this slough, into which they may be attracted by the calls of males already present; at Oak Creek Pond, one mile west of Corvalis, where all frogs entering or leaving were trapped for three years, 14 of 17 frogs were caught in traps adjacent to the outlet of the pond, which flows into Oak Creek.

Males are the first to appear in the breeding ponds. At Oak Creek Pond, the dates of arrival by sex through the 1950-51, 1951-52, and 1952-53 breeding seasons are summarized as follows:

		Dec. 8-14	Dec. 15-21	* Dec. 28 Jan. 3	Jan. 4-10	Jan. 11-17	Jan. 18-24	Jan. 25-31	Feb. 1-7	Feb. 8-14	* Feb. 22-28
1950-51	♂	1		2	2		1		1	1	Tadpoles
	♀						eggs				
1951-52	♂	2	1				1	1		1	
	♀							2			
1952-53	♂	1	1	1							
	♀					1					

*Dec. 22-27 and Feb. 15-21 are omitted, no frogs having entered during these periods.

Behavior in the Water: Evidence of breeding activity occurring during the day is not available. Early-arrival males are prone to bask on the bank during favorable periods, this usually being done in a somewhat protected spot at the water's edge. Such frogs are very shy, leaping into the water and immediately disappearing into the murky depths. Males are considerably less wary at night and will tolerate a flaslight until they can be captured.

Females are more wary in the water, and usually submerge quickly when spotted with a light. The call of *aurora* is so quiet as to be hardly audible beyond 50 feet. The call can best be imitated by attempting to say "Uh-uh-uh-uh" rather rapidly, with the lips compressed, the accent being slightly to more pronouncedly on the first "UH". This call can be given while the frog is submerged. An amplectic female was heard to give a similar call in the laboratory, but calls have been traced exclusively to males in the field. Temperature relationships of the call were not traced extensively, but on two occasions when several males were in full "chorus," water temperatures proved to be 10.6° C. and 9.2° C. On February 2, 1952, a chorus was heard at 8 P.M., and personal notes state that the calls "blended together in a continual low clucking." The calls have a definite ventriloquial quality.

Amplexus is axillary in *aurora*, the male pressing the "thumb" sides of his open "hands" against the lateral aspects of the female's thoracic region. That the male maintains this position tenaciously as long as the clasped object is of proper proportions is attested to by at least two unusual finds. The find of a male *aurora* in amplexus with a male bullfrog (*Rana catesbeiana*) has been presented earlier (Storm, 1952). In this case, it was noted that the forefeet of the red-legged frog had worn two deep abrasions in the pectoral region of the bullfrog. Amplexus was maintained for four days after these frogs were brought into the laboratory. During the spring of 1957, during an afternoon collecting trip, the author came upon a male *aurora* resting at the surface of the water. Closer examination revealed this animal to be "in amplexus" with a floating apple. Cavities approximately 10 mm. deep were worn in the apple by the frog's hands.

The average snout-vent length of nine breeding females is 84 mm. (72-93), and of eleven breeding males, 58.7 mm. (49-65).

During amplexus, size discrepancy tends to bring the vents into juxtaposition.

Based largely on field records of what appeared to be freshly deposited eggs, *aurora* in the Corvallis area may be expected to deposit eggs during January and February. Following the induction of the breeding migration by the proper combination of climatic factors (see above), water temperature is probably the most critical factor for the occurrence of egg-laying. It is difficult to be precise in this matter, but considerable field data indicate that 45° F. (7.5° C.) is near the minimum at which egg-laying begins. In 1953, eggs were deposited in Oak Creek Pond during the night of January 23-24. During this time water temperatures dropped from 52° F. to 45° F. Actual egg deposition has not been observed in this species. Unfortunately, so few *Rana aurora* utilized Oak Creek Pond for breeding that I was never able to obtain complete data as to when a female entered the pond, when her eggs were laid, or when she left. Only two gravid females were caught as they entered the pond (January 13, 1953 and January 31, 1952) and these were never caught again. Records on six males indicated that they first entered the pond on dates from December 9 to January 27, and nine males departed the pond on dates from March 31 to April 9.

Eggs: The eggs are deposited in a rounded plinth, which is attached to some submerged support, most frequently a fairly stiff, more or less vertical stem of some type. The eggs are usually placed within 6 to 15 inches of the water's surface, but often become surfaced or even stranded on the bank as flood waters recede. Fresh egg clumps have a very clear, slightly bluish jelly, but in the usual muddy water, a fine coating of silt soon accumulates, making them inconspicuous.

As viewed from above, the diameter of the egg mass is usually near 6 or 7 inches, although a few masses as small as 3 inches across have been noted. Counts made on egg numbers in six masses (from one locality) give: 541, 648, 811, 918, 1027, and 1081 for each. Variation in numbers is possibly due to the size (age) of the breeding female. Hatching time is closely dependent on water temperature. Eggs kept at a constant temperature of 60° F. (15.6° C.) began hatching in 11 to 12 days, whereas eggs kept at 65° F. (18.3° C.) began hatching in 8.5 to 9 days.

Field conditions are more variable. I was able to observe closely several egg masses from laying to hatching and present the following data: On January 24, 1951, two clumps of eggs were noted in Oak Creek Pond, both having been deposited since the preceding day. These were about 12 feet apart and both were fastened among dead grass stems. Dates and remarks on these eggs follow: January 28—Top of one egg mass frozen in ice at surface. January

30—Top of one egg mass (hereafter called egg mass one) 2 to 3 inches above surface of ice, probably entirely encased in ice. February 3—Damage noted to some surface eggs. February 5—Eggs in both masses at yolk plug stage near bottom of mass, destroyed at top. February 12—Many developing embryos, about 8 mm. long. February 28—Near hatching. March 14—About half of clump hatched. March 15—Still many unhatched. No observations were made during the next 8 days, but by March 23, all the tadpoles were gone, leaving about 10 undeveloped eggs. Water temperatures taken almost daily near the eggs ranged from very close to 0° C. to 15° C. A summary of temperatures follows in which the stated temperature is followed by the number of days on which recorded: 0° C.-3, 1°-1, 2°-2, 3°-1, 4°-2, 5°-1, 6°-3, 7°-5, 8°-1, 9°-5, 10°-6, 11°-3, 12°-4, 13°-3, 14°-1, 15°-1. Although a continuous temperature recording would be much more desirable, it is felt that these indicate the variation to which the eggs are subjected and likewise testify to their ability to survive rather severe conditions. At least three-fourths of this mass hatched after an incubation of about seven weeks. Two other masses deposited on February 13 of this same year in Oak Creek Pond hatched in five and six weeks respectively. These escaped a week of near-freezing weather to which the others were subjected.

Two masses deposited on February 4, 1952 were both completely hatched by March 25, a period of about seven weeks. A similar summary of water temperatures is as follows: 0° C.-3, 1°-2, 6°-1, 7°-3, 8°-6, 9°-3, 10°-5, 11°-7, 12°-3, 13°-1, 14°-3, 15°-4, 16°-1, 17°-2, 19°-1. These figures seem to indicate a higher prevailing temperature during development. However, a rather long incubation period through a considerable temperature fluctuation is indicated.

One egg mass was deposited on the night of January 23, 1953. All were hatched by March 8, an incubation period of just over six weeks. No surface temperatures were taken during this time, but a Bendix-Fries distance thermograph with sensing element located in about two and one-half feet of water indicated a range of 5° to 19° C. Temperatures of over 12° occurred only during the last three days of the incubation period.

Larvae: The egg mass characteristically acquires a greenish cast, owing to an algae invasion, about one week before hatching. Oxygen production by the algae cells causes the mass to float. At the same time the jelly breaks down with the mass spreading out and clumps may be broken away by slight wave action.

For one or two days following hatching, the tadpoles remain crowded near the parent mass, resting on the bottom or more frequently hanging to underwater plants or debris. The average length of the tadpoles at hatching is between 11 and 12 mm. They appear

black, and microscopic examination shows extensive melanophore deposition. The gills are only slightly evident externally as a few simple finger-like appendages protruding from beneath an opercular fold. The external nares appear as minute dark cavities immediately anterior to each eye, which at this stage are simply darkened areas. The mouth opening is small and just anterior to a point midway between the two suckers. The tail tip is symmetrically rounded. Development is rather slow for the first one to two weeks, but certain changes occur as is evident in the following description of a 17.8 mm. larva: Eyes appear black with scattered golden guanophores forming in and around pupil. Dorsal ground color brownish with golden guanophores scattered dorsally and posteriorly to eye and running posteriorly in a rather irregular line to about one-third of the tail length, on each side of the dorsal fin. Dextral spiracle and suckers still evident; mouth poorly developed as yet, but dark beak evident.

Data on growth rates of tadpoles are meager. Tadpoles hatched in Oak Creek Pond on about March 20, 1952, were by April 5 approximately 25 mm. in length, and by April 29, up to 50 mm. By May 23, front legs were not yet apparent and the pond had evaporated to a depth of about one inch. The tadpoles were under continual attack by predacious diving beetles and their survival is highly doubtful. Temperature data is sketchy. Those readings taken were at various time of the day and approximately three inches deep. Temperatures varied from 9° to 27° C., with an average of 14.8 C., and for 35 days between 11° C.-20° C.

Six tadpoles collected from a drying pond on May 9, 1947, and exhibiting varying degrees of hind leg development, measured 59, 37, 38, 56, 43, and 32 mm. in total length. Stebbins (1951) indicates a total length of over 80 mm. for *Rana aurora draytoni* tadpoles, and it is possible that larvae of *aurora* attain this length in more permanent water. In the large pre-metamorphic tadpole, the eyes (dorsal view) are about their own diameter within the head profile, spiracle is sinsitral, and anus opens on the right. Labial teeth are somewhat variable, but are essentially as described by Stebbins for *draytoni* (1951). Viewed under a binocular microscope, the dorsal part of head and body appears covered with a thin transparent layer, which is closely flecked with minute metallic flecks. In addition, there is a fine sprinkling of tiny melanophores. The body wall beneath this transparent "skin" is dark brown with clumps of golden iridescent guanophores. These become more closely spaced postero-ventrally to the eyes. The iris is heavily flecked with brilliant gold-colored guanophores, with an iridescent green on the sclera. Ventrally, the abdomen is a solid iridescent brassy color, and anteriorly there are two or three transverse bands of clumped brassy guanophores. The general effect is a dark brown

tadpole, heavily flecked with metallic markings, and particularly iridescent ventrally.

Recently metamorphosed frogs usually measure between 20 to 25 mm. A 21 mm. individual appeared in life as follows: Grayish-green dorsally, with numerous small black dots; interrupted black line along dorsolateral area; sides lighter, mottled or spotted with black; black line at edge of canthus rostralis and behind eye continuous with dorsolateral line; light line on upper lip evident as in adult; dark diagonal bar across forelimb on anterior side; rear legs mottled and barred with dark; throat obscurely mottled with dark on gray background; belly yellowish-white; undersides of rear legs pale flesh color.

It is probable that most *Rana aurora* tadpoles metamorphose during June and July in the Corvallis area. On May 26, 1947, numerous large tadpoles possessing hind legs were seen moving sluggishly in liquid mud, the last remnant of a drying pond. Metamorphosed frogs leave the water at a time of year that tends to be unfavorable to above-ground activity. It is probably that they aestivate in cracks or in mammal burrows, unless associated with permanent water. Growth during the first summer may be slight, but speeds up as the fall rains enable them to move. There is evidence that they become sexually mature in two years, males are somewhat over 50 mm. in s-v length and females are near 60 mm. at this age. The largest male in the Oregon State College Museum of Natural History collection measures 68 mm. in s-v length, whereas the largest female measures 100 mm.

Summary:

1. The red-legged frog (*Rana aurora aurora*), in the Willamette Valley of western Oregon, begins breeding activities soon after January 1. This activity is initiated by moderate to heavy rains, accompanied by temperatures of near 50° F. or above. Egg-laying occurs at water temperatures above 45° F.

2. Eggs are deposited in rounded masses, attached to submerged stems a few inches beneath the surface. Hatching time is variable, but frequently extends to 6 to 7 weeks under field conditions, during which time the eggs are subjected to much temperature variation.

3. Various stages of the tadpole are described briefly. Metamorphosis normally occurs in June or July of the same season as egg deposition. Larvae seem incapable of transforming before about June 1. Sexual maturity may be attained in two years, when males are about 50 mm. and females about 60 mm. in snout-vent length. Maximum snout-vent lengths in this area have been 68 mm. for males and 100 mm. for females.

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ADDITIONAL RECORDS OF THE EASTERN SPADEFOOT FROM INDIANA.—The only Indiana record of the eastern spadefoot, *Scaphiopus holbrooki*, is for the vicinity of Shoals, Martin County (Swanson, 1939, Amer. Midl. Nat., 20: 713.) Recent collecting has added three more localities.

During the early morning of June 23, 1960, rainfall totalling 5.14 inches was recorded at New Albany, Indiana. That evening about 2 mi. NW of Georgetown (Floyd County), we heard a few calls of the eastern spadefoot from dense undergrowth in flooded lowland along Indian Creek. The spadefoots were associated with great numbers of Fowler's toads, *Bufo woodhousei fowleri*, gray treefrogs, *Hyla v. versicolor*, spring peepers, *Hyla c. crucifer*, and chorus frogs, *Pseudacris triseriata* ssp. At Central Barren (Harrison County), four small to medium sized choruses of spadefoots were heard from flooded cornfields and lawns. Air temperatures during our observations were 80-83° (F). Specimens collected and a tape recording of their calls are in the private collection of the authors.

An additional Indiana locality has been brought to our attention by J. B. Cope of Earlham College and Janet Stone. In June 1956 and July 1957 they observed spadefoots near Elizabethtown, Bartholomew County, following heavy rains. Specimens have been deposited in the Joseph Moore Museum, Earlham College. This record is noteworthy because it is slightly east of the unglaciated plateau and represents the first record of the species from the glaciated portions of Indiana, Ohio, and Illinois. The spadefoot's secretive habits may partly account for the scarcity of records from these states, but it is likely that occurrence is genuinely sporadic. This may well represent another example of a relict whose midwestern distribution was wider during some post-Pleistocene warm, dry period.—*Sherman A. Minton, Jr., Basic Medical Sciences Institute, Karachi, Pakistan* and *Madge R. Minton.*

CANNIBALISM IN *DICAMPTODON ENSATUS*—A variety of animals has been recorded in the diet of *Dicamptodon ensatus*, although no detailed study has been made of its feeding habits. Stebbins (*Amphibians of Western North America*, p. 51, 1951) records several instances of this salamander's feeding on vertebrates, including other amphibians. The larvae of *Dicamptodon* and other ambystomid salamanders are notorious for their cannibalistic tendencies in aquaria although there are no authentic records of this in natural situations.

The following observations on *Dicamptodon* suggest that this species may feed on its own kind in nature whenever the opportunity presents itself. In October, 1957, near Jenner, Sonoma County, California, I had 6 *Batrachoseps attenuatus* and one *Dicamptodon*, approximately 150 mm. in total length, in a quart jar. A second *Dicamptodon*, about 120 mm. total length, was added. Less than ten minutes later as I was about to add another salamander the large *Dicamptodon* was found eating the smaller individual, which struggled violently despite the fact that its head was inside the other's mouth. The attack must have begun almost at once, since both animals showed signs of the struggle. The larger animal hung on tenaciously and they were separated only with considerable effort on my part. It is interesting that no attempt was made on the smaller *Batrachoseps* in the jar, but the presence of another *Dicamptodon* elicited a reaction almost immediately.

In July of 1959, a large male *Dicamptodon ensatus*, 211 mm. total length, was taken near Duncan's Mills, Sonoma County, California. Its summer retreat was under a redwood log about six feet long and four feet in diameter. The log was sunk about 10 inches into the soil and it required six persons to turn it. There were no other amphibians present except the large *Dicamptodon*, which was placed in a quart jar by itself. Several hours later it became warm and the salamander died in the cramped container. When examined, it had partly regurgitated another *Dicamptodon* approximately 130 mm. in total length. The victim was partly digested, but the head was intact, and there was sufficient skin remaining to make a positive identification. There is no evidence that young *Dicamptodon* choose a different habitat from that of adults, so they must be in constant danger from attack by larger members of their own species. It would be of interest to study the behavior of *Dicamptodon* when brought into contact with other members of the species and other species of salamanders. A detailed study of this salamander may show that cannibalism is most prevalent during the drier parts of the year when other food is at a minimum. If cannibalism is common, one wonders what effect this will have on population structure and spatial distribution of age classes within a population.—*James D. Anderson, Museum of Vertebrate Zoology, University of California, Berkeley 4, California.*

Results of Stirnorganectomy in Tadpoles of the African Ranid Frog, *Pyxicephalus delalandi*

ROBERT C. STEBBINS, WILLEM STEYN, AND CYRIL PEERS

Introduction

Shielding or removal of the third eye in several species of lizards was followed by an increase in their activity (Stebbins and Eakin, 1958; Glaser, 1959). An attempt to test the comparable organ in the tuatara (*Sphenodon punctatum*) gave negative results (Stebbins, 1958). The present study tests the effect of removal of the stirnorgan (frontal or Steida's organ) of a tadpole. Whether this organ is strictly homologous with the parietal eye of reptiles is not settled, but clearly in both cases a pineal derivative is involved.

There have been a number of studies of the microanatomy and function of the stirnorgan (Leydig, 1891; Kleine, 1930; Winterhalter, 1931; Oksche, 1952, 1955, 1956; and Kreiner, 1956), but to our knowledge no one has tested the effect of its extirpation (stirnorganectomy) on tadpoles kept under conditions approaching those of the natural environment.

In view of the results with lizards, we have focused attention on reactions to sunlight and locomotor activity. We have also looked for an effect on growth and metamorphosis.

Delaland's burrowing frog (*Pyxicephalus delalandi*) appears to be the ecological counterpart of members of the American genus *Scaphiopus*. It was chosen for the following reasons: The stirnorgan is well developed in both the tadpole and transformed frog. The duration of the tadpole stage is approximately 60 days, offering a study period that would not be unduly extended. Tadpoles in natural ponds were frequently found in warm shallow water near the pond margins where photothermal changes are accentuated. A heliophylic type was desired since it was presumed that the stirnorgan might be a light receptor. The species is hardy in captivity and feeds readily on liver, food that could easily be procured. Finally, the tadpoles are largely independent in their movements. They do not show the pronounced schooling behavior of *Bufo carens* and *Pyxicephalus adspersus*, for example, other species in the area that might have been used in the experiment. As will be explained later, schooling behavior was to be avoided.

The experiment was conducted in an outdoor pool on the grounds of the University of Witwatersrand, Johannesburg, South Africa. A comparison was made between two matched groups of tadpoles from the vicinity of Johannesburg, one stirnorganectomized, the other sham-operated,[1] composed of individuals similar

1. Tadpoles subjected to trauma similar to that experienced by the stirnorganectomized tadpoles but in which the stern organ was left intact.

in size range and stage of development, separated from one another in the pool by a nylon net, in order to prevent mixing. We found it essential to do the experiment in an artificial pool to facilitate recapture of tadpoles for counting and measurement and to protect them from predation. We found no suitable natural pool.

The stirnorgan is usually evident to the naked eye. Its position

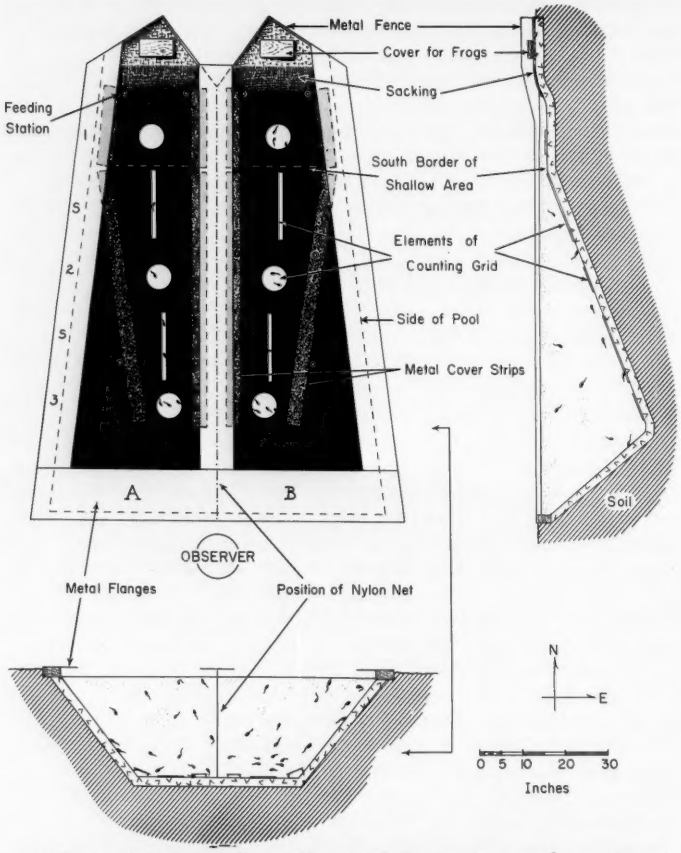

Fig. 1. Diagram of pool in which locomotion and reactions to sunlight were studied in *Pyxicephalus delalandi*. Aerial view, upper left; side view, upper right; cross-section, lower left. In the upper left diagram the grid elements on the bottom of the pool were designated on the sides of the pool (shown on left side only in drawing) in sequence as follows: 1, S, 2, S, 3. The swimways A and B were separated by nylon netting.

is often marked by a gold speck midway between the anterior border of the eyes. The organ is spherical and transparent and lies just beneath the epidermis on a pad of connective tissue, the external surface of which is concave and variously overlaid with guanin which sometimes forms a solid layer. Pigment cells (guanophores and melanophores) in the overlying skin tend to thin out or are lacking. The organ was present in all tadpoles studied, although in advanced larvae and recently transformed frogs it was often difficult to see.

In median sagittal section the stirnorgan of an early tadpole and two recently transformed frogs measure respectively, 117 x 53μ, 115 x 49μ, and 112 x 52μ. A C-shaped cavity (as seen in section) is present, the opening of the C directed away from the epidermis. A single layer of cells forms the outer wall, but the basal part, toward the brain, is over three times thicker than the outer wall; a few cells are suspended in the lumen. Elongate pineal sensory cells are present but not abundant, resembling somewhat those described for *Rana temporaria* by Holmgren (1918). Ganglion and supporting cells, as described by Oksche (1952), appear to be present. There is a scattering of melanic pigment granules throughout the organ. We have not found a stirnorgan nerve (Van de Kamer, 1950; Oksche, 1955).

Experimental pool.—The pool, of concrete and sealed with asphalt emulsion, contained 1,200 liters of water (Fig. 1). The depth of the water at the shallow end was 1 to 1½ inches. A tightly drawn fine mesh nylon net divided the pool into equal parts along the long axis. An 8-inch wide flange of galvanized metal overhung the sides except at the shallow north end, preventing transformed frogs leaving the water except at the shallow end where escape was facilitated by the gentle slope and a covering of moist sacking that extended from the water to a deck a few inches above the water level. The deck was kept moist by capillary action in the sacking and a board propped ¼ inch above the surface of the deck provided cover. On land the two groups of frogs were separated by a metal partition. The frogs were prevented from leaving the area by a galvanized iron fence 3 inches high that skirted the deck. The frog quarters were covered by a wire screen and the tadpole area by 1-inch mesh chicken wire to protect the animals from predation.

Shelters constructed of galvanized metal strips 3 inches wide, painted black, were placed on the bottom on each side of each "swim way" throughout its length. They were elevated ⅜ inch from the bottom of the pool. It was possible, therefore, for a tadpole to swim the length of the pool without exposing itself.

Feeding stations were uniformly distributed throughout each swimway in an attempt to discourage tadpoles gathering at a particular feeding site. Feeding pegs (heavy needles), upon which

pieces of liver of uniform size were impaled, were held in place by a base of plastocene.

In removing tadpoles for study, the pool was drained and the tadpoles caught with a dip net. Handling was uniform. After study they were switched in the swimways.

Selection and Preparation of Study Animals

Selection of individuals for study.—We found insufficient numbers of tadpoles of the same size and stage of development to make two homogeneous experimental groups. Therefore, individuals selected from a heterogeneous group of tadpoles were operated on in matched pairs, one individual stirnorganectomized, the other sham-operated. In this way we were able to compose two closely similar groups, although there was considerable range in size and stage of development in each (Fig. 4, A, Jan. 17). At the beginning of the experiment, the mean and range in head-body length of the stirnorganectomized group was 8.13 mm. (4.4 to 14.0 mm.) and of the controls, 8.18 mm. (4.0 to 13.0 mm.) (Fig. 3, A). Stages ranged from 1 to 6 (Fig. 2, A). A total of one hundred and twenty tadpoles of each surgical type was used. Some *Rana angolensis* tadpoles were unintentionally mixed with the *Pyxicephalus*, 12 among the stirnorganectomized and 9 among the sham-operated groups. In the early stages these two species are difficult to distinguish.

Surgery.—Stirnorganectomy was done under ether anesthesia with a microscalpel and a capillary vacuum tube. The operating stage consisted of a disc of plastocene covered with a thin layer of moist cotton. A furrow accommodated the body of the tadpole and could be changed in size to fit the individual undergoing surgery. The ether was administered by placing a few drops in a watchglass filled with water into which the tadpole was placed. The dish was then covered with a glass plate to prevent rapid evaporation of ether. Since surgery required only one or two minutes, deep anesthesia was not required and most individuals recovered within a few minutes.

A longitudinal incision was made near the right side of the organ and was hooked around a short distance to the rear, in order to make possible lifting of a flap of skin. Extirpation was achieved with gentle suction and the tips of fine forceps. Although there was some blanching of the dura along a line following the course of the knife, probably caused by a concentration of melanin in the cell reservoirs of the melanophores, it is doubtful if the dura was ever penetrated. The melanophore response seemed to be chiefly the result of pressure. It was evident even before the integument had been successfully cut. Bleeding was slight and there was no brain damage. Occasionally a slender translucent thread of tissue came with the

organ, possibly the stirnorgan nerve. The sham-operation duplicated the surgical trauma in an area about 1 mm. to the right of the stirnorgan.

Following surgery the tadpoles were left overnight in an antibiotic solution of mylipen (procaine penicillin) and sulphadiasine

Table 1
Locomotor Movements in Tadpoles[1]

Phase I			Stirnorganectomized			Sham-operated			Group Differences
Date	Duration of observ. (min).		No. of tadpoles	Total movements	Av. per tadpole	No. of tadpoles	Total movements	Av. per tadpole	Movements per tadpole
Jan. 10	46		120	122	1.02	120	116	.97	+ .05
12	65		120	169	1.41	120	170	1.42	— .01
15	110	→	120	147	1.22	120	203	1.69	— .47
17	51		114	220	1.93	114	212	1.86	+ .07
18	132		113	190	1.68	114	262	2.30	— .62
				848 (1016)			963 (1175)		
Phase II									
Jan. 19	56		113	45	.40	113	56	.50	— .10
20[2]	55		112	45	.40	113	15	.13	+ .27
21	30		112	26	.23	111	13	.12	+ .11
22	52		108	86	.80	111	83	.75	+ .05
26	30		97	25	.26	105	8	.08	+ .18
29	20		92	39	.42	93	39	.42	.00
			266 (323)				214 (279)		
Phase III									
Feb. 10	205	→	35	289	8.26	33	149	4.51	+3.75
11	62		33	66	2.00	31	85	2.74	— .74
14	27		18	49	2.88	17	57	3.00	— .12
16	45	→	16	28	1.75	17	6	.35	+1.70
17	80		9	78	8.67	9	34	3.78	+4.89
18	70	→	9	31	3.44	9	22	2.44	+1.00
				541 (557)			353 (374)		

1. More observations were made than are shown here but only those study periods in which one group scored 25 points or more are included. Lower scores were not considered a valid index to activity. Numbers in parentheses are total scores obtained when all observations are counted. Arrows indicate times when tadpoles were switched in runways.

2. After January 20, except for the days preceding switching of tadpoles in the swimways, the numbers of tadpoles indicated as present in the swimways are approximate. Data on emergence of transformed frogs and the closeness of counts on days when tadpoles were removed from the pool, however, indicate that the overall decline in numbers in the two swimways was uniform.

in tap water. Healing appeared to be complete in about 48 hours. The small number of deaths that occurred in the course of the experiment attest to the success of the surgery. The tadpoles were placed in their respective swimways over the period from January 6 to 10 and the first laboratory inspection of the two groups was made on January 16 and 17. In this time only four stirnorganectomized and one sham-operated tadpole had been lost.

At the end of the experiment microscopic examination of the pineal region of sample sham-operated and stirorganectomized animals showed, respectively, no brain damage and that the stirnorgan was absent.

Method of Study and Results

Locomotor activity.—Possible differences in locomotor activity in the two groups were investigated by counting tadpoles seen to cross numbered parts of a counting grid (Fig. 1) placed on the bottom of the pool. Against the discs and strips of white lacquered galvanized metal of the grid, which stood out sharply against the black background of the pool bottom, tadpoles were readily seen, even in deep water. It was possible to detect the tip of the snout or tail of a tadpole that had encroached onto the surface of the grid.

Table 2

Frequency of "Bubbling" by Tadpoles

	Date	Duration of observ. (min.)	Stirnorganectomized			Sham-operated			Group Differences
			No. of tadpoles	Total bubbling	Av. per tadpole	No. of tadpoles	Total bubbling	Av. per tadpole	Bubling per tadpole
Feb.	8	10	51	27	.53	53	10	.19	+.34
	10	35	35	6	.17	33	6	.18	−.01
	11	16	33	65	1.97	31	45	1.45	+.52
	12	73	28	44	1.57	29	24	.83	+.74
	13	57	24	10	.42	26	4	.15	+.27
Totals				152			89		

One point was given for any tadpole that entered a part of the grid, even if only a small portion was seen, and the location on the grid was noted. An individual resting on the grid was counted only once and a tadpole seen to cross a grid element twice in the act of

surfacing to breathe[1] (or "bubble," Table 2) likewise scored only one point when it was certain that only one individual was involved. The grid systems of the two swimways were so close to one another that, from the position of the observer at the south end of the pool, all grid elements could be seen at once. In order to obtain information on possible changes in activity with time of day, counts were made in the morning, at midday, in the midafternoon and on several occasions at dusk under artificial light. To avoid frightening the tadpoles, the approach to the observation post was made cautiously and the observer remained seated quietly during the observation period which usually lasted 25 to 30 minutes.

The movements of the tadpoles across the grid were not completely random. The tendency (although weak) for the individuals to gather at a particular feeding site or shelter in the pool caused variation in scoring in different parts of the grid. However, the many observations, large number of tadpoles, uniformity of conditions in the two swimways, and practice of changing the tadpoles in the swimways, should have minimized the aggregation effect on scoring.

Table 1 summarizes the results of the observations on movements. Statistical tests[2] reveal no significant difference between the scores made at the end of each of the three phases of study. In testing for significance, the scores made on each day of observations were considered to be pairwise dependent (Dixon and Massey, 1957:124-127).

In handling the tadpoles in the laboratory at the end of phase one, the impression was gained that the stirnorganectomized ones were less active than the controls, but such differences were not noted later. No differences between the two groups in activity in relation to time of day were shown.

Breathing.—Toward the end of the experiment we attempted to obtain a measure of activity in the two groups by counting the number of individuals in a given period of time seen to rise to the surface. A single point was given each time the quiet surface of the pool was agitated by tadpole movement. During 5 periods of ob-

1. Excursions to the surface, presumably to breathe air, are a widespread trait among aquatic amphibian larvae. The movements increase in frequency with a rise in temperature. Spurway and Haldane (1953) found that in newts (*Triturus cristatus*) the lungs were generally filled through the nostrils without opening the mouth, but the animals usually discharged a bubble through the mouth as they put the head under. No analysis of gas released at the surface by *Pyxicephalus* tadpoles has been made. Presumably after the lungs form the manner of breathing is comparable to that of the newt. In this paper we refer to the rhythmic trips to the surface to "bubble" as breathing, but it must be emphasized that this has not been proven.

2. Throughout the paper a two-sided t test was used since the data were found to be normally distributed.

servation from February 8 to 13, the stirnorganectomized tadpoles scored 152 points, the controls 88 ($.025<P<.05$). Over this period numbers of tadpoles of the two types were reduced from approximately 50 each to half that number as individuals transformed and left the pool. In *Rana angolensis* (9 stirnorganectomized and 9 sham-operated) tested in the outdoor pool and in aquaria, the stirnorganectomized animals scored 638 and the controls 512 ($.025<P<.05$) over the period February 17 through March 8. All the *Pyxicephalus* had transformed by that time.

Although there is a significant difference between the stirnorganectomized and sham-operated tadpoles, it must be pointed out that the scoring potential of each prior to surgery was not determined, nor would it have been meaningful to do so in view of rapid changes with growth. We, therefore, cannot rule out the possibility that the differences may have been caused by factors other than removal of the stirnorgan.

Temperature conditions and reactions to sunlight.—The gradient in depth of the water provided a photothermal gradient. Even when clean water, largely free of silt, algae, and other organisms, was placed in the pool, illumination of the bottom in the shallows was much more intense than at a depth of two feet. The temperature conditions were similar to those found in natural ponds occupied by *P. delalandi* as judged from occasional temperatures taken in the field. Most readings were made between 8:00 and 11:00 a.m. and 2:00 and 5:00 p.m. and were obtained near the surface at both the shallow and deep end of the pool. A few were taken at the bottom at the deep end. It is probable that the temperatures recorded closely approximate the extremes that were available to the tadpoles in the course of the experiment. The range in 79 temperatures recorded over the period of study was 16.5 to 29.0 (mean 21.5).

As was to be expected, there were greater temperature fluctuations at the surface than in the depths. During a prolonged overcast, after a period of intense illumination, or with the approach of evening, the shallows were cooler than the deeper water, reversing the conditions found when the sun was out. No attempt was made to study separately the reactions of the tadpoles to light and heat. Tadpoles exposed on bright warm days in the shallow part of the pool experienced greater radiation than those exposed in the deep part. Since the counting grid included both areas it was possible to determine relative amounts of exposure to sunlight by comparing scores made by the two groups in the shallows and depths of the pool, but no significant differences were found.

On January 18, in the course of an observation period extending from 2:25 to 3:04 p.m., the bright sunlight that prevailed during the first 10 minutes gradually declined because of gathering clouds.

By 3:00 p.m. there was an exceedingly dense overcast and rainfall. In the first 10 minutes, the stirnorganectomized tadpoles made 50 points, the controls 33. As the sky darkened the former rapidly reduced activity, scoring only 30 points throughout the remaining 29 minutes. The controls maintained nearly even activity and scored 88 points during this period. Converted to movements of tadpoles per minute, in the first 10 minutes the stirnorganectomized group scored 0.04, dropping to 0.01 in the next 29 minutes, whereas the control group remained constant at 0.03. There were 113 stirnorganized and 114 controls in the pool on this date. Unfortunately, other attempts to correlate locomotor activity with changes in sunlight gave negative results but numbers of tadpoles were much smaller then and there were less marked changes in light at times when observations were made.

Growth, rate of development, and timing of transformation.— From time to time all animals were removed from the pool, measured, and the stage of development determined. Measurements were of head-body length and tail in both tadpoles and recently

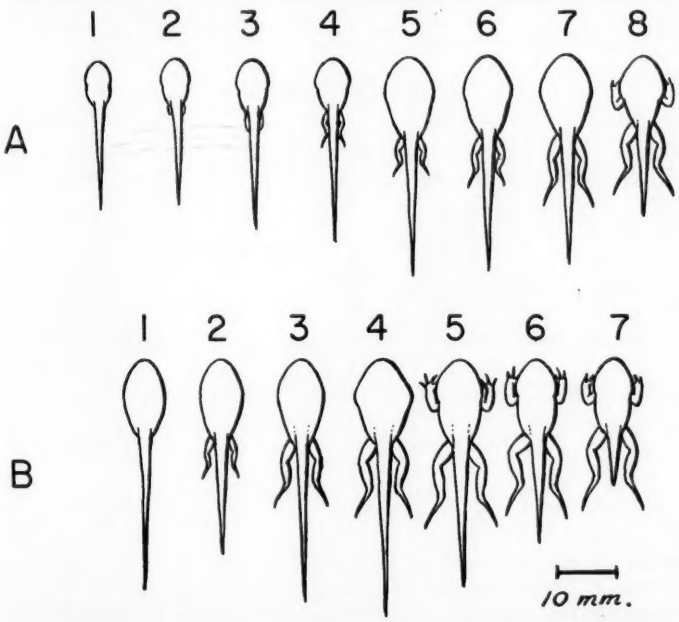

Fig. 2. Developmental stages used in classifying stirnorganectomized and sham-operated tadpoles on January 9 and 17 (A) and February 9 (B).

transformed frogs. The stage of development was determined by comparing each animal with a graded series of stages (Fig. 2). To obtain information on timing of transformation, the board covers of the frog quarters were lifted nearly every day and all individuals found there were immediately preserved.

Growth rate (Fig. 3, A and B) and time of emergence on land (Fig. 5, A) seems to have been the same in the two groups but the movement of frogs to land in the stirnorganectomized group ap-

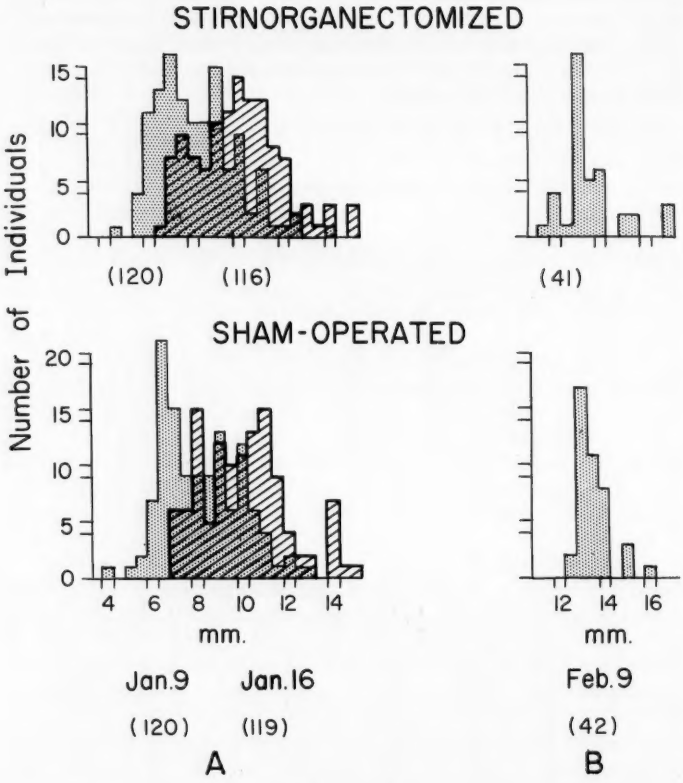

Fig. 3. Growth (head-body length) in stirnorganectomized and sham-operated tadpoles. Size of samples (figure in parenthesis) and dates of measurement are indicated. Measurements made on January 9, at the beginning of the study, shown in stipple, those on January 16 shown in diagonal lines.

pears to have been a little less regular. In the study of growth, head-body length was considered independently of stage of development. Actual measurements (of head-body length) were as follows: January 9, stirnorganectomized, mean—8.13 mm. (range 4.5 to 14.0 mm.), sham-operated, 8.18 mm. (range 4.0 to 13.0 mm.); January 16, stirnorganectomized, 10.0 mm. (range 6.5 to 15.0 mm.); sham-operated, 10.0mm. (7.0 to 15.0 mm.) and February 9, stirnorganectomized 13.6 mm. (11.5 to 17.0 mm.) and sham-operated 13.5 mm. (12.5 to 16.0 mm.).

Rate of development was similar in the two groups. On January 17 the stages observed in both groups ranged from 1 to 8 with the average stage between 3 and 4 (Fig. 4, A). On February 9 both groups ranged from 1 to 7 (Fig. 2, B) with a mean between 3 and 4 for the stirnorganectomized animals and 4 for the sham-operated ones. Except for an initial burst of transformation in the stirnorganectomized tadpoles prior to January 25th (Fig. 5, A), overall

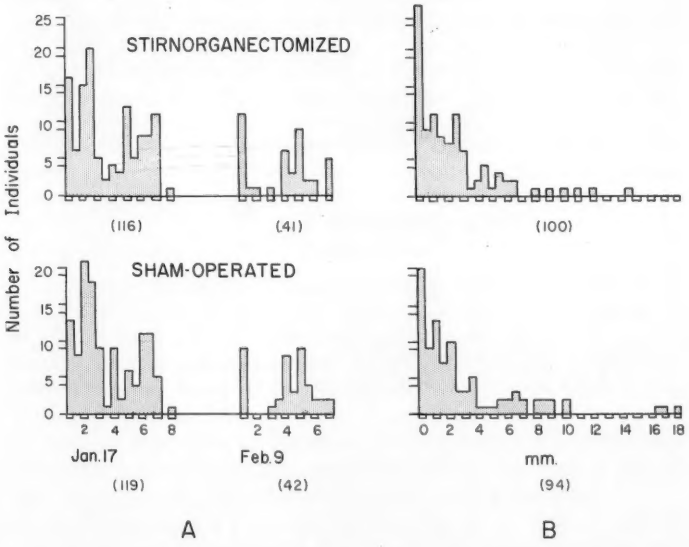

Fig. 4, A. Variation in stage of development in stirnorganectomized and sham-operated tadpoles at check periods on January 17 and February 9. The ordinate indicates numbers of individuals, the abscissa developmental stages shown in Figure 3, A (Jan. 17) and B (Feb. 9).
B. Variation in tail length at the time of emergence on land.

rate of emergence of the two groups was similar. At transformation the stirnorganectomized frogs averaged slightly smaller size than the controls (Fig. 5, B). The former measured 13.6 mm. (range 10.5 to 16.5) and the latter 14.0 mm. (range 11.0 to 18.0) in head-body length. These differences, however, were not significant ($.05 < P < .10$).

Differences in the length of the resorbing tail (Fig. 4, B) at the time of emergence are in the same direction and at the same level of significance, stirnorganectomized 2.3 mm. (0 - 14.5 mm.) and sham-operated 2.9 mm. (0 - 18.5 mm.). In view of the lack of close correlation between size and stage of development, one would not be justified in assuming that body length and tail length are

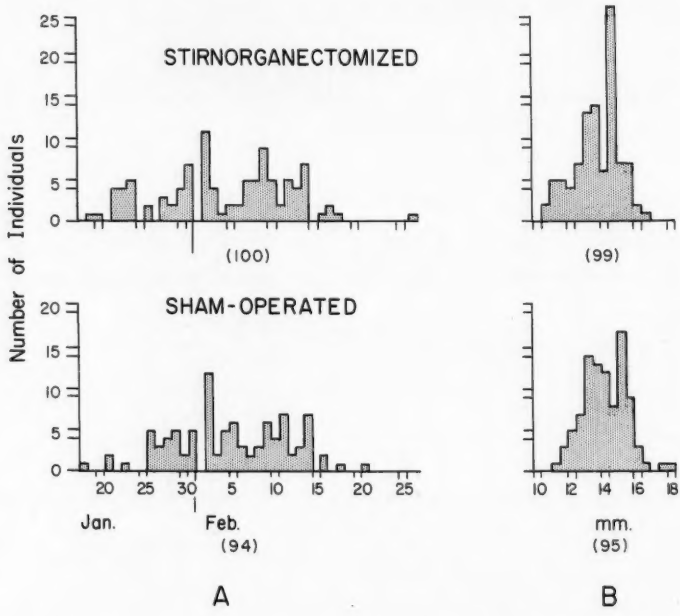

Fig. 5 .A. Rate of transformation as measured by numbers of recently transformed frogs of the two surgical types found under the board cover in the frog quarters on collections days in January and February.
B. Variation in body length in the two surgical types at transformation.

dependent variables. Therefore the result tends to support the validity of the difference in size.

Dermal pigment changes.—Tadpoles kept in the laboratory on a light brown soil background darkened when placed in the outdoor pool where the background was black. Several times in the course of the experiment sufficient red soil, blown into the pool from the surrounding courtyard, accumulated on the bottom to change completely the general tone of the substratum. The tadpoles turned pale in color like those in the laboratory but became black again when the pool was cleaned. The color changes in the outdoor pool rendered the animals inconspicuous against the pond bottom. However, no differences either at night or in the daytime were noted in the color response of the two surgical types. Although Kleine (1930) found no change in the distribution of pigment or capacity for color change in frogs following stirnorganectomy, Bors and Ralston (1951) and McCord and Allen (1917) observed paling of the skin following, respectively, injection and feeding of pineal substance to tadpoles. The pineal substance used for feeding was presumably beef pineal, most probably not homologous with the stirnorgan. Oksche (1952) suggests that in *Rana temporaria* the ground substance for the binding of the melanophore hormone in the dark is produced in darkness by the ganglion cells of the stirnorgan. On a few occasions the color of our tadpoles was noted after sundown; again no differences were evident. In the laboratory handling in connection with measuring and staging, the general tone of pigmentation was noted but no differences were seen.

Summary

Behavior, growth and rate of transformation have been compared in stirnorganectomized and sham-operated tadpoles of *Pyxicephalus delalandi* under seminatural conditions in an outdoor pool subject to natural climatic variation. The study was carried out at Johannesburg, Union of South Africa, at an elevation of 6000 feet in an area where the species occurs naturally.

Results were mostly negative. Stirnorganectomy had no clear effect on locomotor activity, exposure to sunlight, rate of growth and development, time of transformation, or pigmentation.

The frequency of excursions to the surface to "bubble" (release gas or gulp air) was greater in stirnorganectomized tadpoles than in the controls but the possibility of an inherent difference in the two groups, unrelated to removal of the stirnorgan, has not been ruled out.

It would be of interest to test the effect of increased light stimulation. This could be done artifically or by conducting an experiment in a region where natural illumination is intense. If the

stirnorgan in *Pyxicephalus* inhibits activity when the tadpoles are faced with conditions of sunlight that encourage metabolic excesses, the action of the organ should be especially evident under prolonged exposure to light.

Acknowledgements

This study was made possible through a National Science Foundation Senior Postdoctoral Fellowship for the study of the pineal complex (Stebbins) and a grant from the South African Council for Scientific and Industrial Research (Steyn). The support of these organizations is gratefully acknowledged.

The University of the Witwatersrand allowed construction of the experimental pool on University property where the experiment could be conducted with a minimum of disturbance. The study was conducted while Stebbins was a guest of the Bernard Price Institute of Paleontological Research.

Professor B. I. Balinsky aided us in the choice of the experimental animal. Dr. William Gaffey, University of California Department of Public Health, advised on statistical procedures and Mr. John Pun performed the statistical analyses and histological work. Professors Richard M. Eakin and W. B. Quay and Dr. Andrias Oksche have read the manuscript and offered helpful suggestions.

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RETURN OF THE TOAD, *BUFO TERRESTRIS AMERICANUS*, TO THE BREEDING SITE.—While studying movements of Green Frogs and Bullfrogs at the Edmund Niles Huyck Preserve in Albany County, New York, during the summer of 1960, we made the following observations on the American Toad, *Bufo terrestris americanus*, which seem to be worth recording.

At the foot of a bank from which gravel is dug, a temporary pool about 40 feet long, 15 feet wide, and 18 inches deep in the deepest part, was formed from rain water. On June 22 we collected all the toads in the pool, nine calling males, tattooed a white bar across the back of each, and released them the next morning. On the night of June 24 seven additional calling males and a female were seen in the same pool. We collected the seven males, tattooed a white bar across the back of each, and returned them also to the pool. (The female was left undisturbed. She mated successfully and deposited a string of eggs the night of June 24.)

The pond began to dry and by July 6 a single male was the only toad remaining. On July 9 the pond went completely dry. The tadpoles from the successful mating mentioned above had not metamorphosed and were all killed when the pond dried up.

On the afternoon of July 13, a hard rain started which continued throughout the night and most of the next day (July 14). By that night the pond was filled nearly up to its original level and again was visited by calling male toads. We collected every toad present, a total of sixteen males. Thirteen of the sixteen were ones that had been marked there before the pond went dry. It is thus clear that in this case at least the second calling aggregation represented a second period of activity by the individual toads rather than a later period of activity by a second lot of toads.

By July 26 the pond had again dried up. Another hard storm on July 30 refilled it by mid-afternoon and that night a few toads were trilling in the pond. We saw only three, all unmarked males. No toads were seen or heard after August 2, although the water was still very high.

It is interesting that the toads largely stopped calling when the pond started to dry the first time and made no attempt to complete sexual activities in a body of water doomed to extinction. That the breeding season had not terminated is demonstrated by the return of these same toads to call in the same pond two weeks later. We have no knowledge of where the toads went when they left the pond nor do we know if the high percentage of males represents a true sex ratio or merely the indifference of female toads to the calling males. *—Olive B. and Coleman J. Goin, Department of Biology, University of Florida, Gainesville, Florida.*

Aquatic Respiration in *Trionyx spinifer asper*

WILLIAM A. DUNSON[1]

Introduction

This study of the aquatic respiratory processes in the Gulf Coast Soft-shelled Turtle (*Trionyx spinifer asper*) investigates pharyngeal, dermal, and cloacal aspects of underwater respiration. The remarkable ability of turtles to survive while submerged for long periods of time is well known. Lüdicke (1936) reported that one lived under water for eight days. He stated that aquatic turtles respire under water by bucco-pharyngeal movements which force water into and out of the vascular mouth. He also noted that the cloacal bladder expands simultaneously with the lungs, and is concerned with underwater respiration. Carr (1952) reported that soft-shelled turtles have been found to be susceptible to the fish poison, rotenone, in lakes, whereas other turtles are not. Carr said that suffocation by rotenone appeared to be connected with the pharyngeal and anal respiration practiced by soft-shells, but that it was by no means clear why this was so when the surfaces for aquatic respiration were of limited function and merely auxiliary to a pair of efficient lungs.

Agassiz (1860) stated that the skin on the ventral surface of the soft-shelled turtle acts as a respiratory organ, because of its rich network of blood vessels. He demonstrated that aquatic turtles have proportionately much less lung capacity than terrestrial turtles. He stated further that in the pharynx are many fringelike processes which resemble the inner gills of tadpoles and probably have the same function; however, he did not discuss the method of their use. Sager (1856) called attention to the processes in the pharynx of *Trionyx*, and compared them in appearance with the gill filaments of *Necturus* and the inner gills of tadpoles. Gage and Gage (1886) wrote the classic paper on aquatic respiration in *Amyda mutica* (*Trionyx muticus*) and *Aspidonectes spinifer* (*Trionyx spinifer spinifer*). They found that their turtles respired by pharyngeal movements under water, and that a membrane set with filamentous processes, in the mouth, was the organ of respiration. The microscopic structure and extent of the membrane were also described by S. H. Gage (1886) in another article.

Cahn (1937) demonstrated the presence of pharyngeal and anal currents in *Trionyx muticus*. The absence of cloacal bursae in the Trionychidae was explained by Smith and James (1958) as a possible result of the aquatic respiration practiced by this family. This

[1]I wish to express my appreciation to Dr. Alvin Novick, assistant professor of zoology, Yale University, for his advice and criticism of the manuscript. This research was sponsored by a National Science Foundation Undergraduate Research Award given through the Dept. of Zoology, Yale University.

was based on the fact that the Trionychidae and the Kinosterninae are the only groups that have members which hibernate under water and which lack cloacal bursae.

Discussion

Thirty-four experiments on aquatic respiratory processes were carried out with *Trionyx spinifer asper*. The Gulf Coast Soft-shell was chosen because of its availability in the Atlanta, Georgia, area where the work was done. All specimens used were collected by the writer in Nancy Creek in Atlanta, Georgia. They were kept in large tubs containing water and sand. Since the tubs were galvanized, and zinc is toxic to organisms, all the tubs were rinsed out before use with dilute hydrochloric acid, to oxidize the zinc.

To measure oxygen used in aquatic respiration, the turtles were confined under water in a five-gallon aquarium by means of a wood-and-screen partition two inches above the bottom of the aquarium. Water samples of sixty-five cubic centimeters each were taken every hour by a syringe through a mineral-oil film covering the surface of the water. The mineral oil prevented any atmospheric gases from dissolving in the aquarium water. The Winkler method was used to determine the concentration of dissolved oxygen in the sample taken, using fifty cubic centimeters of the water for titration.

To determine the different mechanisms used in aquatic respiration, the pharynx, the skin, and the cloaca were investigated. Of the thirty-four experiments, fourteen measured total respiration, six measured pharyngeal respiration, eight measured dermal respiration, and six measured cloacal respiration. A pharyngeal membrane was already known to be respiratory, but nothing conclusive had previously been proved about the dermal and cloacal role in respiration.

Total respiration was tested by measuring the oxygen used by a turtle in normal condition under water in the aquarium apparatus. Pharyngeal respiration was measured by taping up the cloaca and spreading vaseline over the plastron before testing the turtle in the aquarium. Cloacal respiration was measured by taping up the head and forelimbs of the turtle into its shell and spreading vaseline over the plastron before testing. Dermal respiration was measured by taping both the head and cloaca shut before testing in the aquarium. The cloaca and the pharynx were sealed with waterproof tape lined on the inside with a plastic sheet. No currents were detected passing under the seals on several occasions when dye was inserted in the water. If a seal was loosened by a turtle, the data for that experiment was discarded. The Winkler test for dissolved oxygen concentration in the aquarium water was made at regular intervals for several hours. These results were tabulated, and from them

were computed the cubic centimeters of oxygen used per gram of turtle for each interval. The oxygen use during total respiration for each turtle was compared graphically with that for pharyngeal, cloacal, and dermal respiration for the same turtle.

The hyoid apparatus located in the ventral portion of the neck immediately posterior to the skull, is the means by which water is taken in and expelled from the mouth.

The hyoid apparatus was observed to move sixteen to twenty-

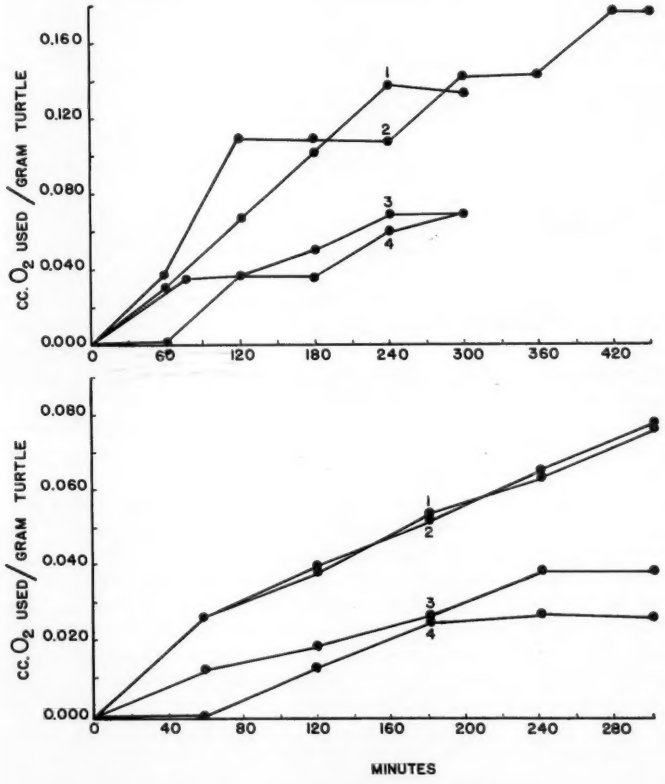

Fig. 1. Aquatic Respiration in *Trionyx spinifer asper*
Upper: weighed 65 grams, 1-pharyngeal, 2-total, 3-dermal, 4-cloacal
Lower: weighed 186 grams, 1-pharyngeal, 2-total, 3-cloacal, 4-dermal

five times per minute when the turtle was submerged. As the hyoid is lowered, the pharyngeal cavity is enlarged, and water enters through the nose and partially opened mouth to equalize the pressure in the cavity. Conversely, when the hyoid is raised, water is forced out through the mouth and nose. The rate of these hyoid movements remained almost constant for any one turtle during its forced submersion. The position of the hyoid and its structure were observed in x-rays and in a dissection made on a specimen which was injected with red and blue latex. In living specimens, numerous fine blood vessels were observed to be distributed over all the plastron and ventral skin. They were particularly concentrated under posterio-ventrally placed folds of skin between the tail and the hind limbs. In the injection made, it was not possible to apply sufficient pressure to inject these dermal capillaries. The cloaca of the turtle dissected was not observed to have a villous-like membrane in it like the one found in the pharynx. Ridges were evident in the cloacal walls, but as the specimen was a female, these were modifications for egg laying.

Pharyngeal respiration was found to be almost as effective in oxygen uptake as the total respiration in four out of five cases tested. Cloacal respiration was less effective than total respiration in six out of six cases tested. Dermal respiration was also less effective than total respiration in five out of five cases tested. Pharyngeal respiration was found to be more effective in oxygen uptake than either dermal or cloacal respiration alone in four out of five cases tested. Figure 1 shows these results in two typical cases. Since the surface area of a turtle would increase less than its volume for a given increase in weight, it would be expected that cubic centimeters of oxygen used per gram of turtle would decrease with increasing turtle weight. It is a well established fact that larger animals are relatively more efficient than smaller ones, because of the proportionately smaller ratio of surface area to volume for a larger animal. This is exactly what was observed in these experiments. Oxygen use per gram in these turtles varied as an inverse function of body weight. Exponential curves were obtained for total, pharyngeal, cloacal, and dermal respiration when oxygen use per gram was plotted as the ordinate against the abscissa of the mass of each turtle in grams. The shape of the curves suggested that oxygen use per gram might be a logarithmic function of the mass of a turtle. This would be true if the points, plotted on logarithmic paper, yielded a straight line. This was found to be the case for total, pharyngeal, cloacal, and dermal respiration, shown in figure 2.

In several cases, turtles drowned during their forced submersion and were revived by artificial respiration, squeezing and expansion of their shells; in later experiments, each of these same turtles respired under water very well. At the end of each experiment,

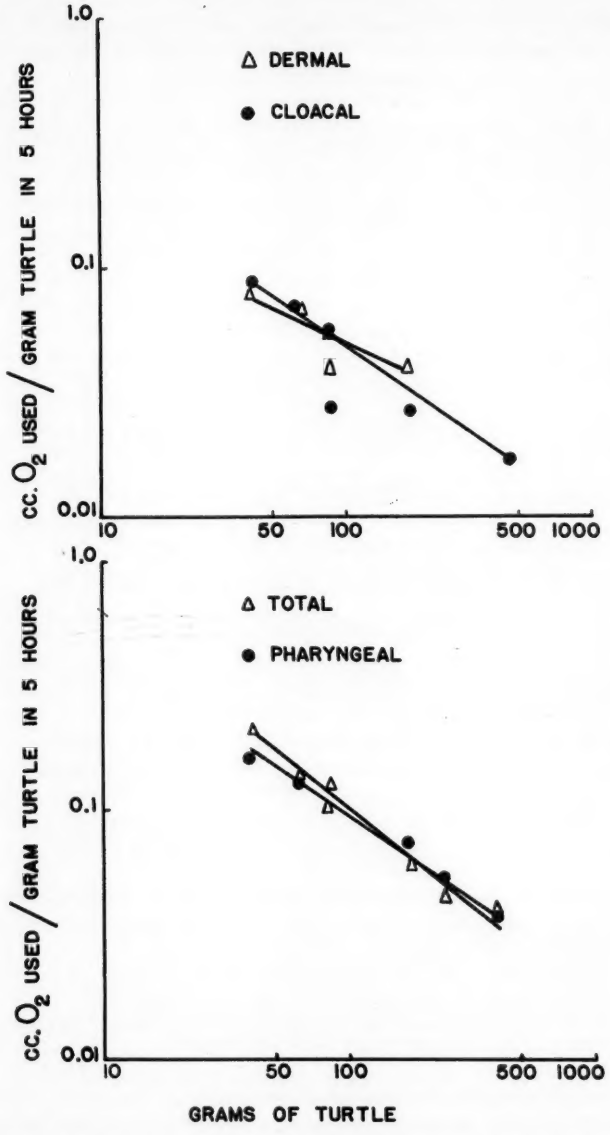

Fig. 2. Logarithmic Plot of Total, Pharyngeal, Cloacal and Dermal Oxygen Use.

however, the turtles were sluggish, and required some time to return to normal activity. The reason that some turtles seemingly did not use their oxygen-absorbing apparatus as well as they could may be due to the fact that they were not used to being confined in such a small place. Most of the turtles would make attempts to escape throughout the experiment, but some were quiet. When a turtle was placed in the water it carried air in its lungs as well as stored intra-cellular oxygen. If the carbon dioxide given off by a turtle while submerged is measured, it will be found to be greatly in excess of what could be accounted for by the free oxygen taken from the water. This excess carbon dioxide can be accounted for only by the two sources of oxygen mentioned above. Gage and Gage (1886), who reported the above experiment, also found that the lungs of a turtle submerged for ten hours showed only a slight trace of either oxygen or carbon dioxide.

Since these experiments were carried out in such a way that the oxygen in the air could not replenish the oxygen removed by the turtle from the water, it cannot be said whether a turtle could survive under water indefinitely if all the oxygen taken from the water were replenished immediately. It is known, however, that turtles spend the winter buried in the mud at the bottom of streams. Presumably the metabolism is lowered greatly during these times and little oxygen is needed. Dermal respiration alone might provide enough oxygen at times like this. Soft-shelled turtles have been observed to remain voluntarily under water for considerable periods of time, but whether or not they are more dependent on aquatic respiration than other turtles is not known.

When a soft-shelled turtle is forced to remain submerged and allowed to have access only to the dissolved oxygen present in a limited amount of water, a time will come when the turtle will not be able to get enough oxygen to satisfy the needs of its tissues. During hibernation the temperature is lower than normal, the turtle's metabolism is lowered, and it needs less oxygen. When the temperature remains constant, however, the turtle builds up an oxygen debt, which consists of the difference between the amount of oxygen needed and the amount taken in. Since cloacal and dermal respiration removed less oxygen from the water than total or pharyngeal respiration, the oxygen debt of the former would be larger. A visual confirmation of the effect of the oxygen debt built up by all types of aquatic respiration was found in the observation of turtles immediately after removal from a prolonged submersion in water. They emitted a gasp when removed from the water, and began respiratory muscular contractions which were greater in magnitude than any observed in normal turtles. These deep breathing movements, which expanded and contracted the volume within the

shell, usually lasted for from five to fifteen minutes, by which time the respiratory movements would subside to normal magnitude.

Summary

Pharyngeal respiration, using currents of water brought in by hyoid movements, is the dominating type of aquatic respiration in *T. spinifer asper*. Either the dermal or the cloacal respiration is sufficient to sustain life during a forced submersion at room temperature of five hours in a closed system. Oxygen use per gram in *T. spinifer asper* varies as an inverse logarithmic function of body mass in grams.

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A SPINY SOFT-SHELLED TURTLE NEST STUDY.—On June 28, 1958, I observed a large soft-shelled turtle (*Trionyx spinifera spinifera*) excavating a nest cavity on the south-sloping, downstream side of a sand bar on a tiny island in the Mississippi River about five miles north of Minneapolis, Minnesota. The process involved some vigorous scattering of the excavated sand in a manner I have not seen reported before. At 5:00 p.m. the turtle took a stance facing away from the water and began digging at a point about two feet above the water and, as later measured, eight feet six inches from the water's edge. The turtle dug alternately with the hind feet. Each foot was engaged in digging for about 25 seconds; then it was withdrawn and the load of sand snapped backward with such force that some of the sand fell well out into the water, indicating that it was thrown a distance of about ten feet. The cavity was completed in about fifteen minutes and the clutch of 17 eggs laid in six minutes. Using the hind feet alternately the turtle covered the eggs in another five minutes and turned about and entered the water at 5:26 p.m.

After the turtle had left the area I excavated the nest, removed five eggs, and determined that the topmost eggs were about five inches below the surface. I then carefully replaced the sand and staked down a ½" mesh wire screen cover over the nest as protection from predators. I inspected the nest site frequently during the late summer but left the eggs undisturbed. The wire mesh, which had been laid directly on the ground, was reshaped on August 30, into a shallow cage to trap any young that might emerge. On October 4 I opened the nest cavity from the side and removed two of the remaining 12 eggs. These had live, well-formed embryos practically ready to hatch but none had broken from the egg. Again the sand was replaced and the nest site was carefully checked for hatchlings several times between October 4 and November 1 when it appeared certain they would not be emerging that fall. High water in the spring usually inundates the site of this nest, but no spring flooding occurred in 1959 and on April 25 I was able to excavate the nest. Eight of the ten eggs contained well-formed embryos but all were dead.

There are several possible reasons for the failure of these turtles to emerge in the fall as is normally the case. My published records (Reptiles and Amphibians of Minnesota, Minn. Univ. Press, 1944, p. 187) indicate that the soft-shelled turtle in this latitude usually lay its eggs from mid-June to about July 6, so this was not an unusually late nesting for this species.The embryos were probably retarded in their development by the unusually cool season. Minneapolis weather records show that June 1958 was 4.9°F below normal; July was 3.8°F below normal; August, 0.1°F below normal. These were the months during which most growth would be expected.

September was 0.5°F above normal and October, 2.7°F above normal but this belated rise in temperature probably was not sufficient to mature the embryos. It is possible that the sun's heat might have been reduced by the presence of the wire screen cage over the nest. To verify this suspicion I again set the same screen in place over the nest site on June 28, 1960. On July 4 the late afternoon temperature at 5" deep under the cage was 0.5° lower than at the same depth outside the cage. Again on July 10 this temperature was found to be 1.5° lower than outside the cage. Although the coolness of the season probably was the major cause of the failure of this nest, the screen may have been "the straw that broke the camel's back" in this case. This effect could be evaluated better if a continuously recording temperature apparatus could be installed in such a nest to determine the total number of degree-hours above the turtle's developmental threshold required to hatch poikilothermic eggs of this type.

This observation indicates by what a narrow margin a species such as this survives at the periphery of its range. Were individuals of this species short-lived, the northern distributional limits would doubtless fluctuate far more than they now do. *W. J. Breckenridge, Director, Museum of Natural History, University of Minnesota.*

"RED LEG" IN A NATURAL POPULATION OF AMPHIBIANS.—For the past 24 years, amphibian collections have been made in Helotes Creek, north of San Antonio, Texas. This creek is spring and rain fed, varying from 5 to 25 feet in width and averaging about 12 inches in depth. During the summer months the creek usually is reduced to semi-isolated pools. From time to time, collections have been made of salamanders (*Eurycea neotenes*) which were well represented in the fauna of the creek. In the fall of 1958 several salamanders were collected that had the disease "Red Leg," which had never been observed in the population before.

Emerson and Norris (J. Exp. Med., 7:32. 1905) stated that the disease occurred endemically in natural populations. Red Leg constitutes a severe threat to laboratory stocks and has been studied by various authors. Sanarelli (Zentr. Bakt. Parasitenik., Orig., 9:193-222, 1891) described the effects of the disease on various amphibia and Russell (J.A.M.A., 30:1442, 1898) reported more extensive analysis of the organism and toxic reactions.

The name *Red Leg* is derived from the capillary dilation of the lower abdomen and inner thighs of animals infected with *Pseudomonas hydrophila,* a member of the Proteus group of bacteria. As the disease progresses, apparently all the organ systems are involved with large hemorrhagic areas over the entire body as well as septic thrombi and miliary abscesses. The disease is

practically 100% fatal to a laboratory population although carrier animals have been observed.

On November 20, 1958, 29 salamanders (*Eurycea neotenes*) were collected in the creek and returned to the laboratory. During the collecting, the creek temperature was 20° C. Within six days, several of the animals had died. Examination indicated extensive hemorrhagic areas throughout the body. Smears from these areas were cultured and subsequently identified as *P. hydrophila.*

December 3, 1958, the authors again visited the stream and observed the amphibians over a one-mile segment of the creek. Apparently all individuals were infected. Dead salamanders (*Eurycea neotenes*) and frogs (*Rana pipiens* and *Acris crepitans*) were floating in the water. Several salamanders were observed to be very near death and all live amphibians observed had symptoms of the disease. *Rana* tadpoles were also infected with the organism.

A brief visit January 2, 1959, showed little if any change from the previous condition.

The population again was observed June 7, 1959, during which time the creek had been reduced to semi-isolated ponds with only a slight flow between them. In many cases the ponds were completely isolated. Close observation of the fauna did not reveal any Red Leg symptoms. It is thought that the isolation of the ponds allowed new individuals to build up the population in the absence of the infective organisms. It also is possible that a high percentage of these remaining salamanders was immune to Red Leg.

During the period covered by this report, the disease appeared in a laboratory stock of toads. In excess of 100 individuals representing approximately 15 species of the genus *Bufo* were infected. Smith (Science, 112:274-275, 1950) utilized chloromycetin in treatment of the disease in *Bufo marinus.* He found an initial dose of 5 mg./100 g. body weight (orally) followed by 3 mg./100g. twice daily for five days was effective in curing the animals. Similar treatment was used on our stock and the progress of the disease was halted. Two weeks later, a new strain of the organism appeared which was resistant to chloromycetin. The progress of the new strain was checked by an intraperitoneal dose of 10 mg/g. body weight of achromycin V followed by 5 mg./g. twice daily for seven days.—*Don Hunsaker II and Floyd E. Potter, Jr., University of Texas.*

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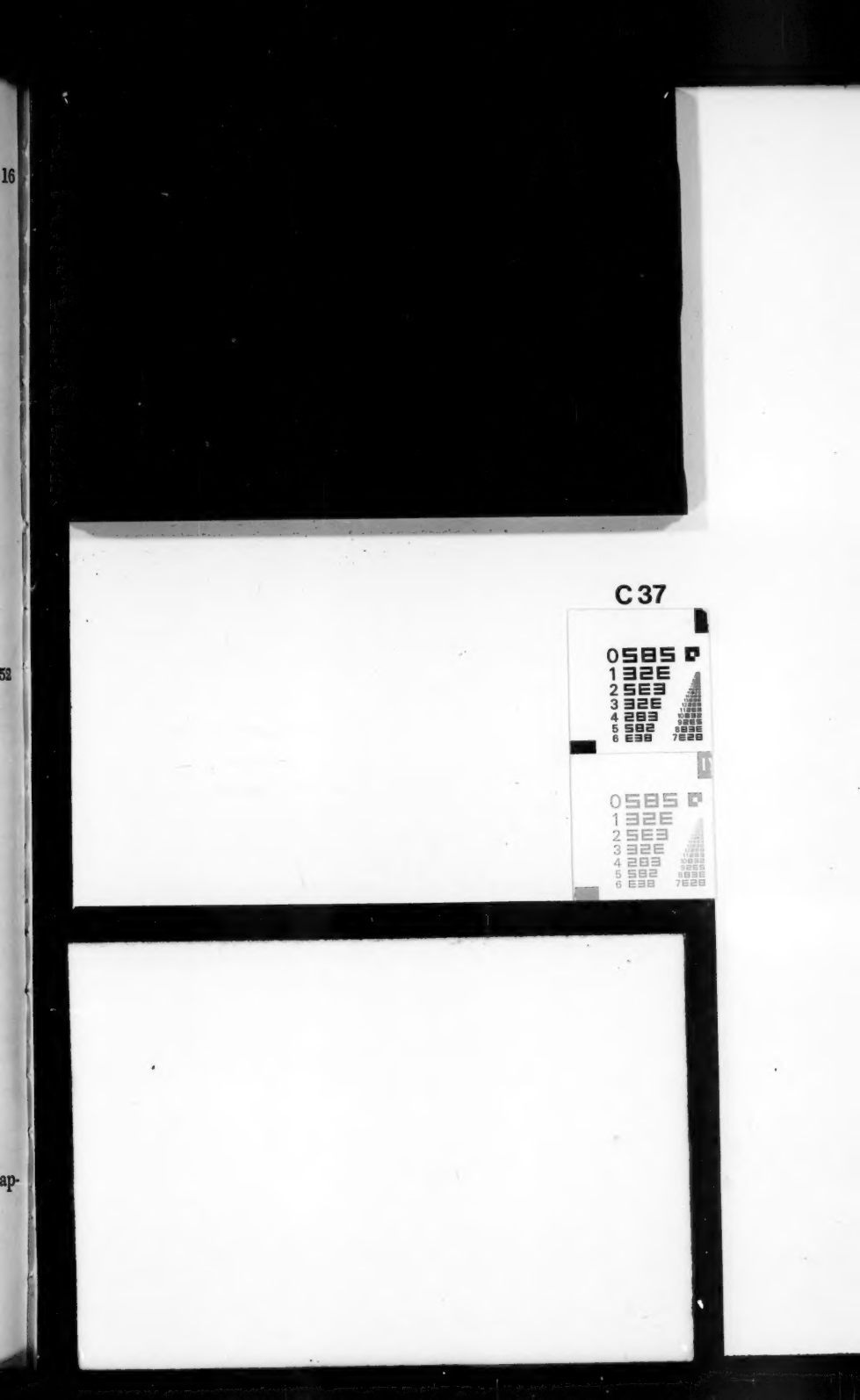
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